Development of a concept for the sustainable management of Baltic Sea beaches

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Abbreviations

AB: accessible beach

BSD: beach at Behrensdorf

CCA: canonical correspondence analysis

NSG: completely closed off nature conservation area

NSGH: nature conservation area with accessible lower beach but closed off backshore and foredunes

PSII: Photosystem II

SCH: beach at Schleimuende

STA: beach at Stakendorf

Zusammenfassung

Strände unterliegen extremen natürlichen Stressfaktoren, wie Wind- und Wellenenergie. Zudem sind sie vielseitigen anthropogenen Einflüssen ausgesetzt. Insbesondere die intensive touristische Nutzung tritt in Konflikt mit Tier- und Pflanzenarten, die eng an den Lebensraum Strand angepasst sind. Das Ziel der vorliegenden Studie ist es, ein Konzept für ein nachhaltiges Management der Ostseestrände Schleswig-Holsteins zu entwickeln. Dabei sollen sowohl die Maßnahmen zur Optimierung ökologischer Funktionen der Strände als auch die sozialen Belange berücksichtigt werden.

Um die Vegetation unterschiedlich genutzter Strände zu charakterisieren, wurde die Artenzusammensetzung von 15 Strandbereichen an der südlichen Ostsee in den Sommern 2011, 2012 und 2013 in Form von Transekten vom Strandwall zur Wasserlinie untersucht. Die Ergebnisse zeigten, dass frei zugängliche Strände einen erhöhten Anteil von Ruderalarten (Artemisietea vulgaris und Molinio-Arrhenatheretea) und einen Rückgang an typischen Strandpflanzen der Klasse der Honckenyo-Elymetea aufwiesen. Außerdem hatten die Strandnutzung und die Distanz zum Wasser einen signifikanten Einfluss auf die räumliche Verteilung von Pflanzeneigenschaften. So besaß die Vegetation frei zugänglicher Strände einen höheren Anteil an Pflanzen mit einer geringeren mittleren Wurzeltiefe und einer eher mesomorphen Blattanatomie. Beide Eigenschaften können die ökologischen Funktionen des Strandes unter anderem durch Änderungen der Sedimentfixierung beeinflussen.

Charakteristische Strandpflanzen wie *Atriplex prostrata, Honckenya peploides* und *Crambe maritima* wurden in Experimentalfelder an drei verschiedenen Stränden angepflanzt und mit geringen Trittstärken von 0, 1 und 2 Tritten d^{-1} m^{-2} belastet. Die Ergebnisse zeigten eine Abnahme im Zuwachs der Biomasse der einjährigen Pflanze *A. prostrata* nur zu Beginn der Trittbelastungen und keine Auswirkungen auf das Samengewicht. *C. maritima* wies eine signifikante Verringerung der Blattlänge auf und hatte eine reduzierte Überlebensrate. Da sich geringe Trittbelastungen deutlich nachteilig auf die Populationsgröße von *C. maritima* auswirkten, wurden der obere Strandbereich und die Vordüne, in denen *C. maritima* in der Regel wächst, als besonders sensitive Zonen gegenüber Trittbelastung bewertet.

Zur Ermittlung der Raumansprüche von Arthopoden wurde der Raumbedarf, die Raumnutzung und die Populationsdynamik von drei terrestrisch jagenden Lycosidae (*Arctosa cinerea, Arctosa perita* und *Pardosa agricola*) durch Fang-Wiederfang-Untersuchungen in zwei Naturschutzgebieten an der Ostsee erfasst. Die Ergebnisse offenbarten, dass sich die Größe des Raumbedarfs von *A. cinerea* zwischen den untersuchten Stränden unterschied. Die Größe des minimalen komplexen Polygons von Männchen an einem schmalen Strand war 143 ±22 m^2 (Weibchen: 165 ±13 m^2). Dieser Wert war signifikant geringer als der Raumbedarf der Spinnen an einem breiteren Strand mit einer größeren Steinbedeckung von 12 % (Männchen: 183 ±13 m^2; Weibchen: 179 ±48 m^2). Insgesamt wurden alle Spinnen häufiger im oberen Strandbereich gefangen. Die Schätzung der Populationsgröße ergab, ein Maximum im Mai und ein Minimum Ende Juli. Außerdem wurden die Bewegungsmuster von *A. cinerea* in einem Naturschutzgebiet und einem frei zugänglichen

Strandbereich direkt beobachtet. Diese deuteten darauf hin, dass Spinnen, die gestört werden, größere Umwege laufen und ihre Laufrichtung zum Meer hin ausrichteten.

Interviews mit regionalen und überregionalen Stakeholdern aus drei Gemeinden in Schleswig-Holstein zeigten, dass eine Verbesserung der Situation der Ostseestrände grundsätzlich als notwendig erachtet wurde, die Ideen zur Gestaltung von Maßnahmen jedoch divergierten. Ein kompletter Ausschluss der Strandnutzung wurde immer kritisch angesehen, da finanzielle Einbußen bei den Einnahmen aus dem Tourismus befürchtet wurden. Insbesondere der Zugang zum Wasser wurde als Grundvoraussetzung jeglicher Maßnahmen am Strand angegeben.

Die Arbeit verdeutlicht, dass bereits geringe Störungen durch Menschen die Flora und Fauna der Strände empfindlich beeinflussen und negative Auswirkungen auf die ökologischen Funktionen des Strandes als dynamischen Lebensraum haben. Dies fordert ein nachhaltiges Strandmanagement, das sich auf die Entwicklung einer integrierten regionalen Küstenraumplanung konzentriert. Hierdurch sollen Bereiche der touristischen Nutzung identifiziert sowie der Ausschluss von ökologisch besonders empfindlichen und wertvollen Strandabschnitten aus der Nutzung aus Gründen des Naturschutzes ermöglicht werden.

Abstract

Beaches are exposed to strong natural stress factors, such as high winds and waves as well as a number of human uses. Among the latter, the intensive use by tourists competes with the area demands of specialised species. The aim of this study is to develop a concept for the sustainable management of Baltic Sea beaches in Schleswig-Holstein, which includes measures for optimizing ecological functioning and integrates social demands.

In order to characterise the effects of different intensities of beach use, the vegetation of 15 beaches of the southern Baltic Sea was investigated in Germany during the summers of 2011, 2012 and 2013. Results revealed that differences in species assemblages originated from an increased proportion of ruderal species (Artemisietea vulgaris and Molinio-Arrhenatheretea) and a decrease in typical beach species of the class Honckenyo-Elymetea. Tourism access and distance to the shoreline had decisive influence on the spatial distribution of selected plant traits. Plant traits at accessible beaches showed, among other things, an increase of plants with a lower average root depth and a mesomorphic leaf anatomy. Both traits might significantly affect the ecological function of the beach by changing the dynamics of sand.

Characteristic beach species such as *Atriplex prostrata, Honckenya peploides* and *Crambe maritima* were planted in experimental fields at three different beaches and exposed to low impacts of 0, 1 and 2 steps d^{-1} m^{-2}. Results indicated that the annual plant *A. prostrata* showed a decrease in plant growth at the beginning of the trampling period, but no effects on seed weight due to trampling pressure. *C. maritima* revealed a reduction in plant growth and plant survival. Trampling pressure explicitly affected population dynamic of *C. maritima* negatively. Therefore, the upper beach area and the foredune as the main growing zones for *C. maritima* were regarded to be particularly sensitive areas to human access.

Similar studies were done on spiders. Home range, distribution and population dynamics of three species of Lycosidae (*Arctosa cinerea, Arctosa perita* and *Pardosa agricola*) were observed by mark-recapture experiments at two nature conservation beach areas at the Baltic Sea in order to estimate the area demand of beach spiders. Results revealed that home range size of *A. cinerea* varied between beaches. Size of minimal complex polygons of males at a narrow sandy beach was 143 ±23 m^2 (females: 165 ±13 m^2) which was significantly smaller than at a broad beach with about 12 % stone coverage (males: 183 ±13 m^2; females: 179 ±48 m^2). The general distribution of all spiders showed a higher use of the upper beach areas than of the lower beach areas. Estimates on population size of the three Lycosidae during summer revealed the highest population size in May and lowest at the end of July. In addition, the movement behaviour of *A. cinerea* was observed at a nature conservation area and an accessible beach area. Direct observation of the movement patterns indicated that disturbed spiders run more detours and focus their movement seawards, where they will be confronted with non-suitable conditions. This study underlines the sensitivity of predatory arthropods of beach habitats to human disturbance and identifies the importance of the upper beach area, in particular.

Workshops and interviews with regional and super-regional stakeholders in three municipalities in Schleswig-Holstein revealed that an improvement of Baltic Sea beaches was seen as necessary; however, concrete ideas were contrary. In general, feared financial losses from tourism caused

reluctance to a complete exclusion of beach access. In particular, access to water was stated to be a basic requirement of any conservation measure at the beach.

In summary, this thesis shows the huge negative effect of human disturbance on beach flora and fauna and its impact on beach functioning. These findings encourage concepts of sustainable beach management focusing on well-constructed coastal spatial planning for areas of tourist use as well as for sensitive beach areas closed for nature conservation.

Chapter 1

Impact of tourism on the ecology of Baltic Sea beaches – a general introduction

Coastlines are dynamic ecosystems that are driven by wave energy, tides and wind. Regular flooding events, exposure to wind and sediment instability challenge beach organisms. Flora and fauna occupying the shore are highly adapted to these harsh conditions and, thus, are often endemic for this habitat type (Brown and McLachlan 1990; Martinez and Psuty 2004; Jędrzejczak 2005; Defeo and McLachlan 2005; Acosta et al. 2009; Irmler 2012). With distance from the shore sand transport and sand burial decreases, whereas the availability of organic mass, groundwater and nutrients increases (Brown and McLachlan 1990). Species of flora and fauna form a sequence due to their tolerance and resistance towards common natural disturbances. Closest to the shore at the area where drift line material deposits during winter, annual pioneers (Cakiletea maritimae) create a first barrier against the impact of the shore (Isermann 2004a; Figure 1.1). Perennial plants and grasses develop in more sheltered conditions at the elevated shore (Isermann 2004b). Here, the main fixation of sand takes place, which, in turn, initiates the development of foredunes by the landward deposit of sands.

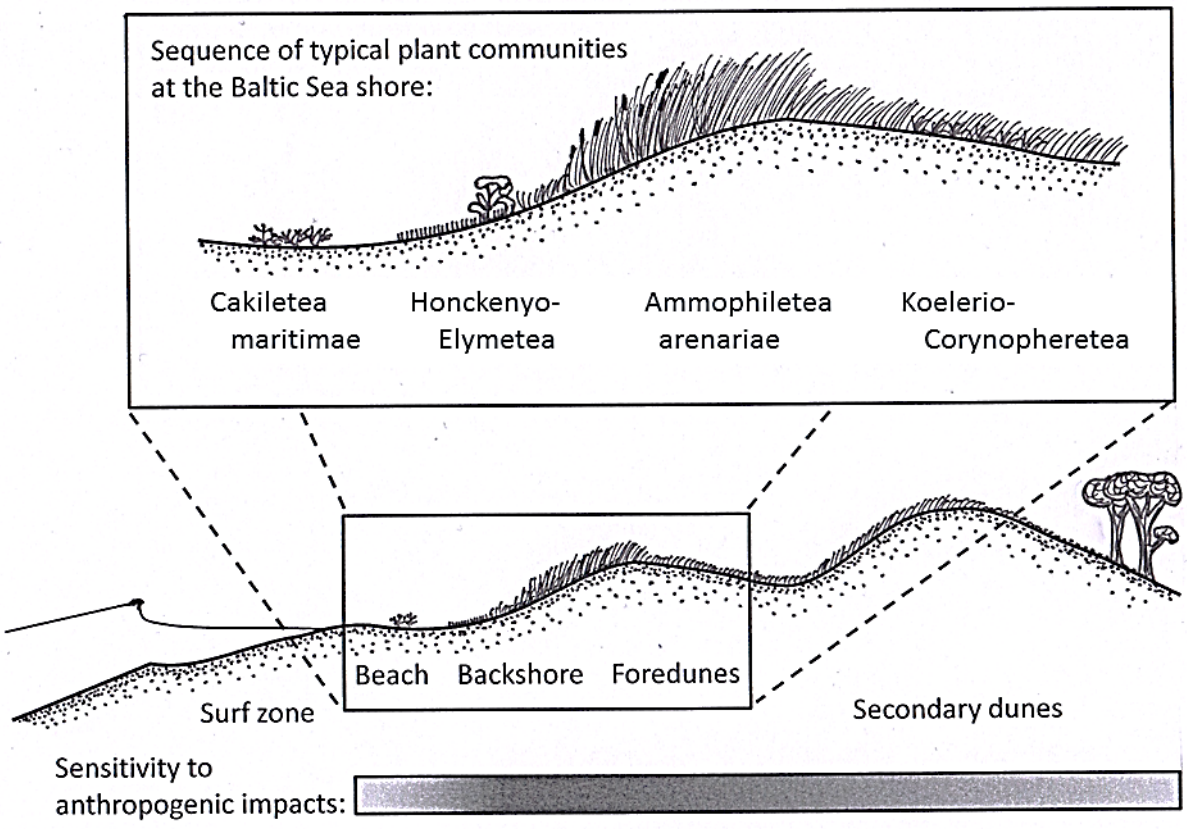

Figure 1.1: The coastal sequence of the typical sandy beach plant communities of the Baltic Sea. (Nomenclature from Dierßen et al. (1988); sensitivity gradient to anthropogenic impacts from Brown and McLachlan (1990); black: very sensitive to human disturbance; white: less sensitive to human disturbance).

Marine as well as terrestrial fauna populate the beach. While marine fauna depends on water saturated sands in the transitional zone, some terrestrial species such as birds (e.g. sand plovers (*Charadrius hiaticula*)) or wolfspiders (e.g. *Arctosa cinerea*) need the beach as main habitat where reproduction and brood care can take place. In contrast, other species (e.g. *Bactra suedana*; Ivinskis and Rimšaitė 2005) that live in the dunes use the beach as a food source. Beaches and dunes are linked by the transport of sand and nutrients from the beach as well as the influence of groundwater and fauna from the dune area (Brown and McLachlan 1990). Thus, research on beach processes, especially if they are connected with erosion patterns, helps to understand dune ecology.

1.1 Anthropogenic impacts on beach and coastal ecosystems

The fragile construct at sandy coastlines is strongly affected by humans. Besides coastal defence systems, harbours, military and industrial use that intensively destroy natural coastal habitats, beach ecosystems have a high recreational value for humans (Barbier et al. 2011; Haller et al. 2012). Thus, they are of great importance for the economy in terms of tourism. Beach tourism leads to direct mechanical impact on beaches by tourists. Additionally to direct tourist impacts, beach organisms are challenged by beach nourishment, beach cleaning and building of accommodations for tourists. In addition, roads and paths for easy beach access are created through the hinterland and the dune system segregating the area (Brown and McLachlan 2002; Schlacher et al. 2007; Defeo et al. 2009).

Over the last few decades, global interest in beach processes has grown. The primary reasons for this are climate change and expected sea level rise. They will severely increase the pressure on beaches by inundation of the shore, greater wave activity and coastal squeeze (Defeo and McLachlan 2005; Defeo et al. 2009; Dugan et al. 2010). Furthermore, climate change is expected to extend the bathing season in the southern Baltic Sea region by enhancing favourable weather conditions for tourists (EU 2008; Matzarakis and Tinz 2008).

Worldwide, research focuses on identifying dune and beach anthropogenic driven modifications. Studies have already shown a loss of vegetation cover in trampled dune systems (Hylgaard 1980; Andersen 1995; Lemauviel and Rozé 2003; Pickering and Hill 2007; Hesp et al. 2010; Santoro et al. 2012) and an increased number of endangered species living at dunes and beaches where mainly tourist use of these habitats can be accounted for (Scott 1976; Davenport and Davenport 2006). Brown and McLachlan (1990) analysed an extreme increase in sensitivity towards human disturbance from the water to the primary dunes identifying the backshore and foredune area as main zone endangered by tourism at the coastline (Figure 1.1). Still, focused research on the effects of direct anthropogenic impacts on beaches is rare (Dugan et al. 2012).

Mechanical impact of human trampling causes a cascade of different effects (Figure 1.2). Liddle (1975) assumed the force of an average standing man to be 200 g m^{-2}. Dynamic shearing forces of a walking person cause direct downslope displacement of soil (Quinn et al. 1980). Thus, trampling not only compacts soil, but also initiates soil erosion (Quinn et al. 1980). According to the intermediate disturbance hypothesis, low levels of disturbance increase habitat patchiness patterns (Connell 1978). This would increase species diversity by creating new habitats for species in formerly densely vegetated ecosystems. Nevertheless, effects of soil erosion at beaches are more intense, because it can induce the abrasion of sand and retreat of foredunes (Raabe 1973; Ciccarelli

2014). Trampling stress on plants mobilizes assimilates and reduces rhizomes and above-ground biomass (Liddle 1975; Fritz et al. 2004; Puijalon et al. 2008; Figure 1.2). This affects the survival of the plants as well as their reproduction, germination and establishment (Liddle 1975; Fritz et al. 2004). Insects at beaches are directly influenced by death, the loss of food sources and the destruction of burrows, which leads to species death and changes in species composition (Schierding et al. 2011; Irmler 2012; Schierding et al. 2013). Consequently, this cascade links the mechanical impact of human trampling on the beach to changes in conservation and amenity value of beach sites as well as changes in beach ecological functioning.

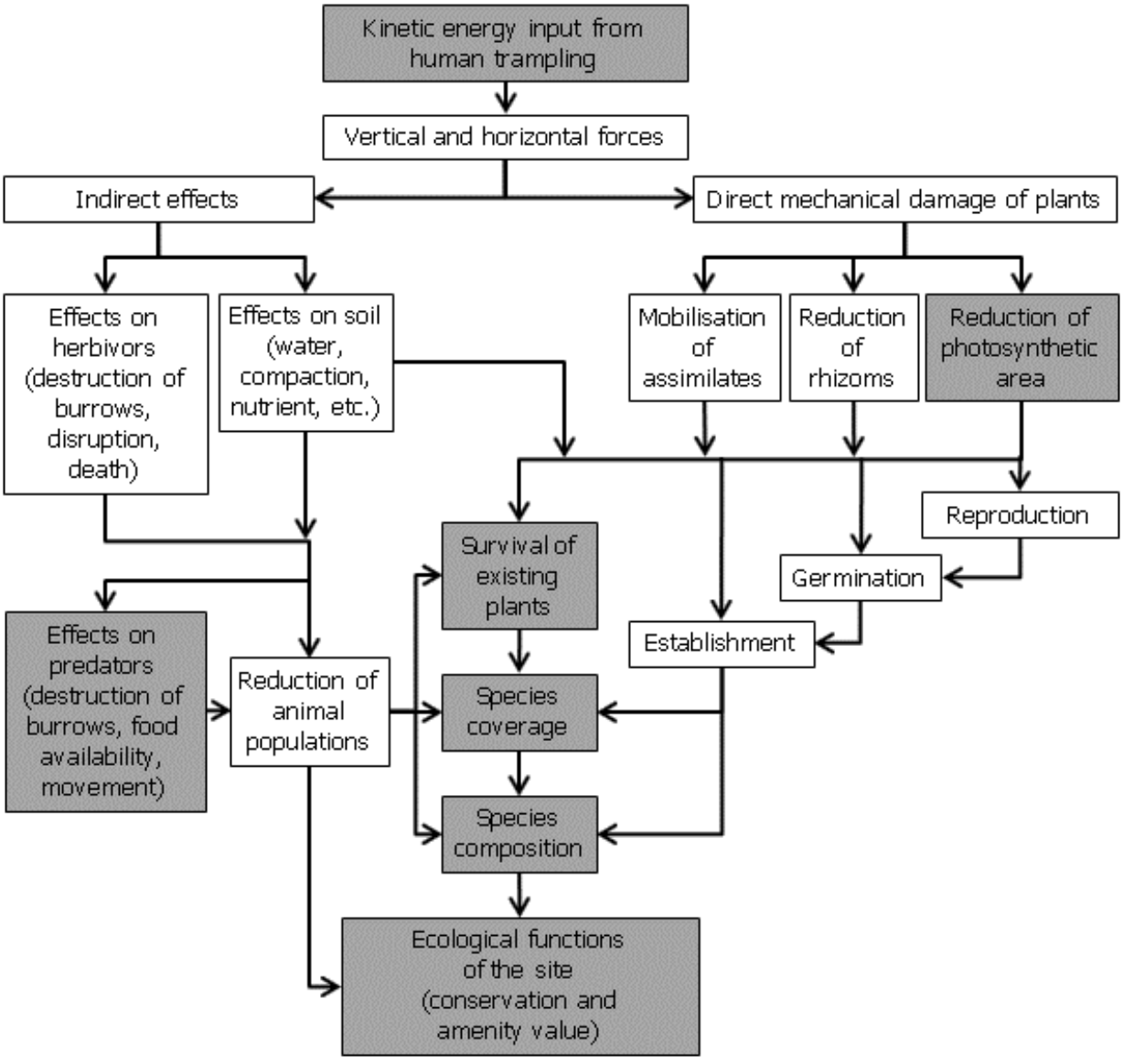

Figure 1.2: A logical model of some of the ecological effects of trampling with causal relationships indicated by arrows (changed from Liddle 1975). Effects observed in this study are highlighted in grey colours.

1.2 The Baltic Sea beaches – Study area

The Baltic Sea was formed during the Weichselian glacial period by glaciers, submergence and emergence of land (Schwarzer 2010; Niedermeyer et al. 2011). Nowadays, Scandinavia still emerges iso-statically while the southern coast is sinking at a rate of about 2 mm $year^{-1}$ (Schwarzer 2010). The enclosed condition of the Baltic Sea lessens the tidal range. Instead, waterline and ocean movements are dominated by wind - and storm - driven shifts (Schwarzer 2010).

Main sediment transport takes place by current and wave movements along the shore. Sediments erode from abrasive coastlines like cliffs or result from seashore abrasion. Subsequently, they are transported parallel to the coastline until they accumulate, forming new lagoons, spits and dunes (Schwarzer 2010; Niedermeyer et al. 2011). Cliffs, material load, currents and wave energy regulate this process. Even at accumulating beaches, seasonal changes between summer and winter lead to erosion processes during winter (Niedermeyer et al. 2011).

The Baltic Sea coast of Schleswig-Holstein is approximately 536 km long (MELUR 2013). About 122 km are cliffs with just a short shore at the foot of the cliff. 121 km have been altered for the construction of dikes for coastal defence. 293 km are either totally obstructed for harbour, marina, industrial and military use or consist of more or less natural sandy and gravel beaches where tourism claims main interests (MELUR 2013). More than 5 million tourist arrivals were ascertained at the German Baltic Sea coast in 2013 (StatA-MV 2014; StatA-SH 2014). An further increase in tourism is expected due to proposed elongation of warm summer periods because of climate change (EU 2008). According to the "Landesentwicklungsplan Schleswig-Holstein", beaches are defined as primarily tourist areas; however, touristic areas are supposed to alternate with natural and scenic sites (IMSH 2010). This objective leaves a wide interpretation and does not solve the conflict between ecological demands and tourism. Additionally, one goal of the new strategy for tourism in Schleswig-Holstein aims at the promotion of ecological and sustainable tourism (MWAVT 2014) which supports the search for solutions to this conflict.

In Western Pomeranian, large areas of the Baltic Sea are under protection as national park areas (Nationalpark Vorpommersche Boddenlandschaft and Nationalpark Jasmund). At these areas, the natural coastal dynamic as well as characteristic biocoenosis are protected. In comparison, only some small coastal sites af the Baltic Sea in Schleswig-Holstein are protected as nature conservation areas allowing no human access (e.g. Naturschutzgebiet Bottsand, Naturschutzgebiet Schleimuende). In some conservation areas, human access is only restricted during the breeding season of birds (e.g. Naturschutzgebiet Kleiner Binnensee bei Behrensdorf); in other areas, only dunes, not beaches, are considered to be protected sites (e.g. Naturschutzgebiet Bewaldete Düne bei Noer). In Germany, several coastal plants that grow at different distances to the shore are endangered (Berg et al. 1996; Mierwald and Romahn 2006), such as *Eryngium maritimum* and *Lathyrus maritimus*. In addition, spiders like *Arctosa cinerea* or *Philodromus fallax* that live in close vicinity to the shore are threatened by anthropogenic impacts (Hoerschelmann et al. 1996; Lemke et al. 2013). Some species, e.g. *Cicindela maritima* that requires large unattended sandy beaches, have vanished in almost all of their former habitats at the coasts in Schleswig-Holstein (Irmler 2010). Müller-Motzfeld and Suikat (1996) have predicted that coastal defence may lead to an absolute habitat loss of endangered beetles, while tourism was considered as the second greatest threat.

1.3 Research questions and outline of the study

The need to understand biological processes resulting from trampling on sandy beaches arises from the necessity of the development of suitable management methods for conservation (Liddle 1975; Dugan et al. 2012; McLachlan et al. 2013). This study aims to identify the primary impacts of trampling and tourist accessibility on beach ecology. There is a great need for crucial guidelines for a sustainable management of Baltic Sea beaches, which include essential ecological conservation measures as well as necessary social demands. The study is implemented in the project "Development of a concept for a sustainable management of Baltic Sea beaches" funded by the Deutsche Bundesstiftung Umwelt and the Lighthouse Foundation. In this project, experiments and observations on flora and fauna at differently managed beaches of the Baltic Sea coast are used to evaluate ecological processes and demands of typical and endemic plants and arthropods at the beach (Figure 1.3). The survey of the sociological study on stakeholder interests and the observation of behaviour of beach visitors are not included in this thesis (Figure 1.3). That part of the project is available in Seer et al. (2015a). Nevertheless, outcomes of that part of the study are introduced in the fifth chapter of this thesis, which is concerned, with the framework of concepts on beach management.

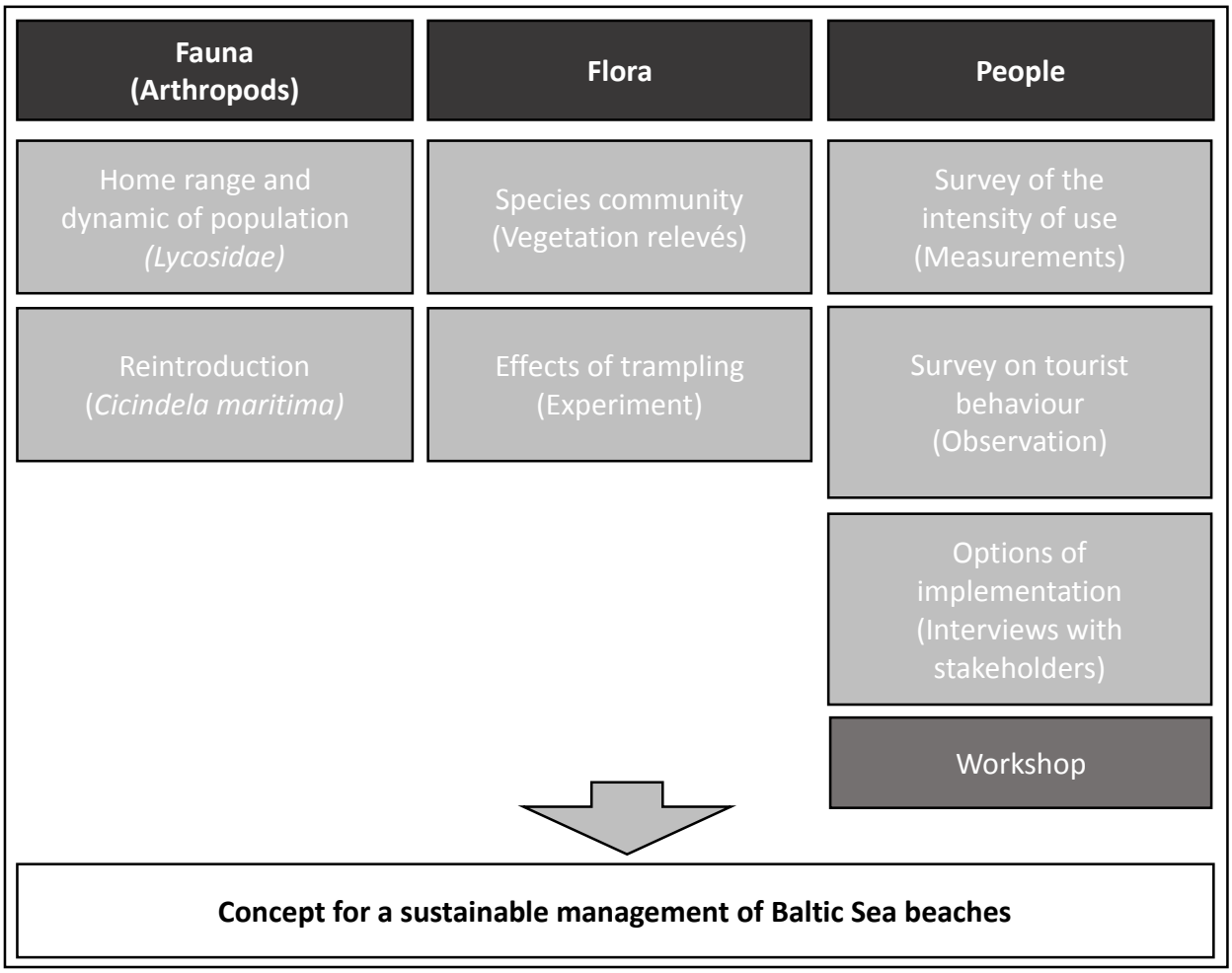

Figure 1.3: Main components of the project to develop a concept for a sustainable management of Baltic Sea beaches.

In the following chapters, this thesis answers main ecological questions concerning sustainable beach management:

The impact of tourism on vegetation structure is assessed in the chapter "Beaches under pressure – effects of human access on vegetation at Baltic Sea beaches". The influence on vegetation structure as well as shifts in plant species composition and plant traits were evaluated at beaches with different levels of tourist accessibility. Furthermore, we discuss how the functioning of ecological beach processes is altered due to changes in vegetation.

In the chapter "Effects of trampling on three beach plants at the Baltic Sea" the influences of trampling on plants are evaluated in detail by an experiment with controlled simulated trampling on *Atriplex prostrata, Honckenya peploides* and *Crambe maritima*. Direct effects of human trampling on plant growth, photosynthetic productivity, reproduction and survival were analysed as indicators of human impacts on ecological functions of beaches.

To take the area demands of the fauna at beaches into account, three species of Lycosidae (*Arctosa cinerea, Arctosa perita* and *Pardosa agricola*) were observed as representatives for arthropods at beaches. Home range, population size and movement patterns were surveyed at two Baltic Sea beaches to assess the localization and minimal size of required conservation areas. Additionally, movement patterns of *A. cinerea* were observed at a closed conservation area and an accessible beach. Details are discussed in the chapter: "How much space is needed for spider conservation? Home range and movement patterns of wolf spiders (Aranea, Lycosidae) at Baltic Sea beaches".

Integrating principles and guidelines derived in previous chapters as well as from literature which lead to a concept for sustainable management of sandy Baltic Sea beaches are summarized in "Tourism and near-natural beaches at the Baltic Sea – a contradiction?".

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Picture A: Conservation beach area on the island of Langenwerder.

Picture B: Intensive tourism beach area near Zingst.

Chapter 2

Beaches under pressure
- effects of human access on vegetation at Baltic Sea beaches

Abstract

Questions

How do cover, richness and composition of plant species vary according to different levels of beach access? What shifts in plant traits occur along gradients of tourism intensity? What recommendations regarding the sustainable management of Baltic Sea beaches can be drawn?

Location

Southern Baltic Sea beaches in Germany

Methods

In this study, the species composition of vascular plants on beaches with differing accessibility to tourists were analysed at the south-western Baltic Sea coast. In total, 894 vegetation plots were evaluated in order to determine vegetation changes along the sea-inland gradient due to different levels of human accessibility at beaches. Relevés were conducted as repeated transects from the beach ridge to the shore. Shifts in vegetation characteristics due to different levels of tourism access were analysed at the level of plant communities and plant species traits.

Results

Species richness did not differ significantly between levels of accessibility. Vegetation cover significantly increased with distance to the shore and was highest in the upper shore area of closed beaches (52.0 ±2.7 %). Corresponding to the increase in beach access, we observed an increase in ruderal species and a decrease in typical beach species of the vegetation class Honckenyo-Elymetea. Tourism access and distance to the shoreline had decisive influence on the distribution of plants with selected plant traits. In particular, at accessible sites, a loss of plants with leaves with great degree of scleromorphy was indicated.

Conclusions

Increased beach access results in a loss of typical beach plant species. Changes in vegetation characteristics are considered to alter the function of the beach ecosystem. Based on these results, we derived spatially-differentiated management measures for excluding the most sensitive beach areas from tourism.

Nomenclature:

Wisskirchen and Haeupler (1998) available electronically at www.floraweb.de

2.1. Introduction

Under natural conditions, the morphology of beaches is mainly the result of sediment budget as well as sea and wind dynamics: flooding, light availability and temperature decrease while humus content, soil moisture, soil stability, and acidity increase with an increase in distance to the shoreline (Passarge and Passarge 1973; Acosta et al. 2009; Peyrat and Fichtner 2011). Beach vegetation is patchy and is low in species diversity but contains a great number of rare and endangered species (Acosta et al. 2009). Composition of flora and fauna consists of species adapted to these stressful habitat conditions (Garcia-Mora et al. 1999; Isermann 2004a/b). Thus, the species of the Cakiletea maritimae class dominate near the shoreline. This plant community consists of robust nitrophilous facultative halophytic annual species such as *Atriplex prostrata* or *Cakile maritima* (Lemauviel and Rozé 2003; Isermann 2004a). Species of the class Honckenyo-Elymetea thrive further from the shore and are seldom affected by seawater during summer (Isermann 2004a; Labuz and Grunewald 2007). They usually have succulent leaves, which provide a high water storage capacity, resistance to wind erosion and sand burial (Salisbury 1952; Garcia–Mora et al. 1999; Labuz and Grunewald 2007). Grassy species of the Ammophiletea arenariae dominate at a greater distance from the sea (Isermann 2004b). They usually form a slightly elevated beach ridge of accumulated sand, which contributes to coastal protection.

This natural vegetation gradient is currently suffering under anthropogenic impacts. More than 5 million tourist visited the German Baltic Sea coast during 2013 (StatA-MV 2014; StatA-SH 2014). Beaches are highly affected by tourism since that is where activities such as water-related sports are concentrated (Haller et al. 2011). Changes in the ecology of beach ecosystems caused by human pressures, such as trampling, are observed worldwide (Brown and McLachlan 1990; Schlacher et al. 2007; Defeo et al. 2009; Dugan et al. 2012; Acosta et al. 2013; Malavasi et al. 2014). Therefore, examination is needed to determine whether or not near natural beach vegetation can still be developed and serve main ecological beach functions even under the pressure of tourism (Andersen 1995; Schlacher et al. 2007; Defeo et al. 2009; Dugan et al. 2012). Previous studies have analysed the overall effects of trampling on beaches and primary dunes. These studies have shown a reduction of species cover (Kutiel et al. 1999; Lemauviel and Rozé 2003; Hesp et al. 2010; Ciccarelli 2014) and changes in species composition (Andersen 1995; Grunewald 2006). Species richness either increases when human impact is low (Grunewald 2006; Grunewald and Schubert 2007) or decreases when trampling intensity is high (Ciccarelli 2014; Malavasi et al. 2014). In contrast to these studies, our analysis also includes plant traits and links them to the ecological functioning of beaches. According to Tilman et al. (1997), changes in species traits can significantly alter particular ecosystem processes and affect ecological functioning, encouraging the focus on the study of plant trait patterns in disturbed beach vegetation. A main function of beach vegetation is the reduction of wave and wind energy and the fixation of sediments (Garcia-Mora et al. 1999; Defeo et al. 2009; Barbier et al. 2011; Fenu et al. 2012). Thus, beach vegetation generally provides and develops habitat and biodiversity by allowing less robust plants to establish in areas where sediments are already stabilized and salt influence is low (Garcia-Mora et al. 1999; Isermann 2004b; Fenu et al. 2012). Furthermore, food sources for terrestrial and semi-terrestrial fauna are provided (Isermann 2004a).

This study analysed classes of plant community and plant traits on Baltic Sea beaches differing in three levels of accessibility to visitors. Besides accessible beaches with low visit intensity, we documented vegetation data of totally closed beaches and beaches with only a closed upper shore.

Closing the upper beach area could be a compromise between nature conservation and tourism. Beaches highly frequented by visitors were not observed because of the lack of any vegetation at these sites. In this study, we aim to answer the following questions: 1) How do cover, richness and composition of plant species vary according to different levels of beach access? 2) What shifts in plant traits occur along gradients of tourism intensity? 3) What recommendations regarding the sustainable management of Baltic Sea beaches can be drawn?

2.2 Material and Method

2.2.1 Study sites and field methods

In total, 894 vegetation plots at 15 beaches with three distinct levels of accessibility to visitors were assessed during the summers of 2011, 2012 and 2013 (Figure 2.1; Table 2.1). Sites were placed at the Baltic Sea in Schleswig-Holstein (14) and Western Pomerania (1). Five beaches were closed nature conservation areas and, thus, not accessible to tourists (NSG). Three beaches were nature conservation areas with closed backshore and fore dunes, but with access to lower shore and water (partly closed nature conservation area: NSGH). Seven beaches were accessible for visitors, but were not frequently used because of the secluded location and rarity of nearby tourist facilities such as parking lots, toilets or shops (AB). Drift line material was not removed for beach cleaning at any of these beaches.

Species composition was recorded by using a transect design along the sea-land gradient (Figure 2.2). At each beach, 10 transects with a minimum distance of 10 m apart were surveyed. Each transect consisted of six 4 m² plots from the top point of the beach ridge (yellow dunes) heading successively towards the shoreline (distance: f-a; Figure 2.2). Total vegetation cover was estimated as a percentage of the plot. Species cover and composition of phanerogams were recorded using the modified Braun-Blanquet-scale (Reichelt and Wilmanns 1973). The content of stones and sand of soils was estimated as percentage coverage.

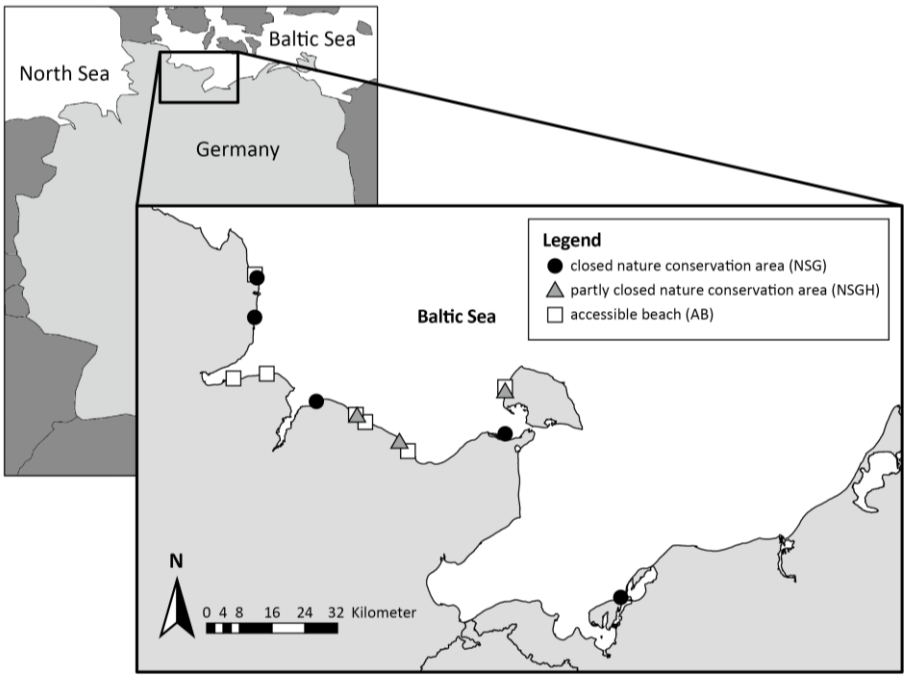

Figure 2.1: Map of study sites along the southwestern Baltic Sea.

Table 2.1: Site conditions at observed Baltic Sea beaches (AB: Accessible beach; NSG: Nature conservation area with closed access; NSGH: Partly accessible nature conservation area).

	Site	Beach access	Coordinates (first transect)	Stone coverage	Beach width (m)	Dune condition and hinterland
1	Behrensdorf	AB	54°20'01.23" 10°38'54.87"	10 - 20 %	16.5 - 20.0	beach ridge and grassland area
2	Behrensdorf	NSGH	54°21'09.53" 10°37'05.09"	10 - 20 %	14.0 - 20.0	beach ridge and small dike
3	Bottsand	NSG	54°25'25.32" 10°16'55.05"	30 - 40 %	17.2 - 19.8	secondary dunes
4	Fehmarn	AB	54°29'01.53" 11°00'41.34"	30 - 40 %	18.5 - 22.6	beach ridge and dike
5	Fehmarn	NSGH	54°28'43.6'' 11°00'39.8"	40 - 40 %	17.2 - 19.0	beach ridge and dike
6	Graswarder	NSG	54°22'47.89" 11°01'22.78"	40 - 50 %	31.9 - 38.9	beach ridge and dry grassland area
7	Hohenfelde	AB	54°23'19.41" 10°29'11.29"	40 - 50 %	26.0 - 31.0	beach ridge; trail and agricultural grassland
8	Langenwerder	NSG	54°01'35.62" 11°29’19.05"	< 10 %	10.0 - 16.0	beach ridge and grassland area
9	Lindhoeft	AB	54°28'00.58" 09°57'48.93"	40 - 50 %	14.4 - 16.8	beach ridge and wooded cliff
10	Schleimuende	AB	54°41'44.32" 10°01'27.37"	< 10 %	14.0 - 20.0	beach ridge and dike
11	Schleimuende	NSG	54°41'42.17" 10°01'32.91"	< 10 %	10.0 - 17.0	large beach ridge and grassland area
12	Schwansene See	NSG	54°36'20.74" 10°01'38.69"	40 - 50 %	20.0 - 29.3	beach ridge and lake
13	Stakendorf	AB	54°24'17.40" 10°26'24.04"	< 10 %	17.0 - 24.0	small dunes and dike
14	Stakendorf	NSGH	54°24'10.02" 10°26'42.13"	< 10 %	20.0 - 28.0	beach ridge and lake
15	Surendorf East	AB	54°28'53.43" 10°05'36.42"	30 - 40 %	24.1 - 27.3	beach ridge and wooded cliff

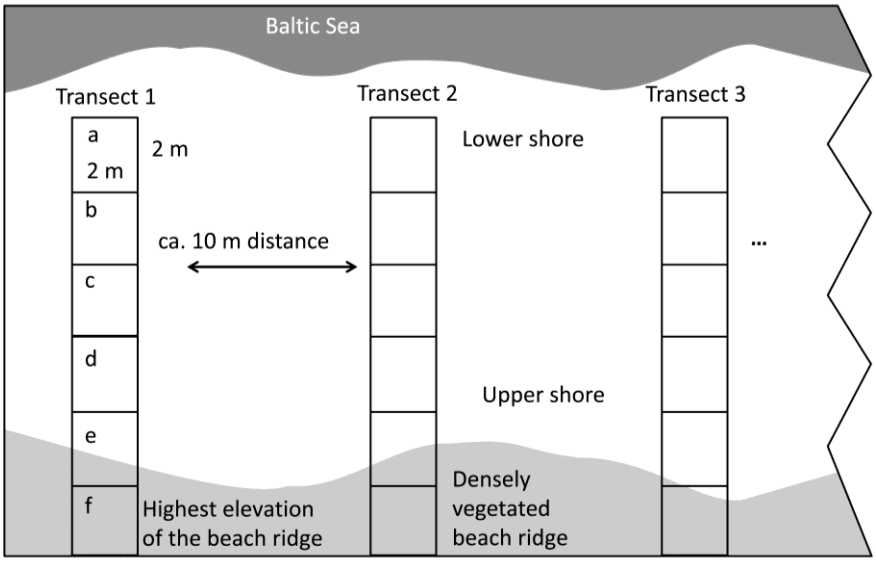

Figure 2.2: Layout of the design of vegetation relevés. At each beach, 10 transects were surveyed, all of which included 6 plots (2 x 2 m) running from beach ridge to shore and were placed at a minimum distance of 10 m to each other

2.2.2 Species composition

The relative cover of plant species of typical plant communities was used to characterize the beach ecosystems at the Baltic Sea and assess the conservational value of different beaches. (Dierßen et al. 1988). We defined the characteristic species of the classes Cakiletea maritimae (R. Tx et Prsg 1950) and Ammophiletea arenariae (Br.-Bl. et Tx. 1943) as target communities (cf. Isermann 2004a; Isermann 2004b). We also considered the class Honckenyo-Elymetea (Tx 1966) to be a target community group, because of substantial morphological and functional differences from the Cakiletea maritimae such as perennial growth. Species of the frequently occurring classes Koelerio-Corynopheretea (Klika in Klika et V. Novàk 1941), Artemisietea vulgaris (Lohmeyer et al. ex von Rochow 1951) and Molinio-Arrhenatheretea (R. Tx. 1937 em. R. Tx. 1970) were also classified. Species that could not be assigned into one of these communities were summarized as "others".

2.2.3 Plant traits

Plant traits were chosen to reflect the response of plant distribution patterns to beach accessibility. All chosen plant traits are significant for plants populating sandy Baltic Sea beaches (Garcia-Mora et al. 1999; Cornelissen et al. 2003; Table 2.2). We chose life form (Raunkiaer 1934) as a trait to describe the whole individual plant. Raunkiaer's life form types are known to be a robust predictor for plant response to mechanical disturbances by describing the location of its perennial organs (Lavorel and Garnier 2002, Cornelissen et al. 2003). Clonal growth (rosette/tussock – erosulate plant) was included among traits, because Sun and Liddle (1993) described tussocks and prostrate plants to be more tolerant towards disturbance. As an essential feature at the beach, we expected a high degree of scleromorph leaves, since they can withstand shearing and burial by sand as well as drought and salt influence (Garcia-Mora et al. 1999). Thus, the degree of plants with scleromorph leaves was also taken into account. Root depth was included to describe below-ground features; roots support sand fixation but can be significantly damaged by trampling

(Boudreau and Faure-Lacroix 2009; Cornelissen et al. 2003). Regenerative traits were considered to be vectors of dispersal as well as indicators of competitiveness within the plant community (Cornelissen et al. 2003). In this analysis, the type of reproduction (mainly vegetative – mainly generative) and seed mass classes (dry matter weight) were chosen as regenerative traits. Species traits were derived primarily from the BiolFlor database (Klotz et al. 2002) unless otherwise specified (Table 2.2). To reduce the number of input variables, some of the traits were grouped into fewer classes than given by the databases (Table 2.2).

2.2.4 Data analysis

For data analysis, the Sqlite3 database [engine version: 3.6.16 (2007)] with the SQLiteStudio management system (http://sqlitestudio.one.pl/) as container of the relevés was applied. The statistical software R version 3.1.2 (R Foundation for Statistical Computing, Vienna, AT, USA) was used to analyse data. Braun-Blanquet-values of vegetation relevés were transferred into mean percentage cover (Dierschke 1994). Relevé trait means were calculated using the weighted mean of each functional trait with the square rooted vegetation cover per plot. Correlations of traits, except for Raunkiaer's life form, were checked with a spearman matrix regression. The data evaluation of species cover, species number, cover of each community group and trait began with the definition of an appropriate statistical linear mixed effect model (Verbeke and Molenberghs 2000). The data were heteroscedastic due to the levels of beach access (use), distance to the shoreline (dist) or beach site (beach) based on a graphical residual analysis. The statistical model included use (NSG; NSGH; AB) and dist (a-f, Figure 2.2) as well as all their two-fold interaction as fixed factors. Beach and transect were regarded as nested random factors. Based on this model, an ANOVA was conducted. After this, multiple contrast tests (Bretz et al. 2011) were performed in order to compare the levels of the influence factors.

The three uppermost plots of each transect (distance d-f) were differentiated according to species assemblage by directly corresponding them to distance to the shore and the degree of accessibility with a canonical correspondence analysis (CCA). The plots of the lower shore (a-c) were neglected because of high zero inflation of the dataset. CCA was chosen as constrained ordination method because of rather heterogeneous data (Lepš and Šmilauer 2003).

Table 2.2: Investigated plant traits and categories for the plants of species assemblage and their data source.

Plant functional trait		Category	Class value	No. of species	Data source
Whole-plant trait	Lifeform	Chamaephyte	1	120	Raunkiaer (1934); Klotz et al. (2002)
		Geophyte	2		
		Hemicryptophyte	3		
		Phanerophyte	4		
		Therophyte	5		
	Clonal growth	rosette plant	1	120	Klotz et al. (2002)
		hemirosette plant	2		
		erosulate or hemirosette plant	2.5		
		erosulate plant	3		
Leaf trait	Leaf anatomy	succulent leaves	1	120	Klotz et al. (2002)
		scleromoph leaves	2		
		helo-, meso- or hygromorph leaves	3		
Below-ground biomass	Rooting depth	down to 50 cm deep	1	104	Salisbury (1952); Kutschera (1960); Kutschera and Lichtenegger (1982, 1992); Kleyer (1995); Duuren et al. (2003)
		down to 100 cm deep	2		
		deeper than 100 cm	3		
Regenerative traits	Reproduction	by seed	1	120	Klotz et al. (2002)
		mostly by seed	2		
		by seed and vegetatively	3		
		mostly vegetatively	4		
		vegetatively	5		
	Seed mass	< 0.2 mg	1	120	Kleyer (1995); Klotz et al. (2002); Hintze et al. (2013)
		0.21 - 0.5 mg	2		
		0.51 - 1.0 mg	3		
		1.01 - 2.0 mg	4		
		2.01 - 10.0 mg	5		
		> 10.0 mg	6		

2.3. Results

2.3.1 Species richness, cover and composition

Vegetation relevés revealed a total of 136 species. Total species richness within vegetated plots was between 1 and 19 species per plot. Species richness at the lower shore area did not differ significantly between levels of beach accessibility. Highest mean species richness was detected in the upper beach area of partly closed off conservation areas (Table 2.3, 2.4). This differed from lower species richness in totally closed off beaches, which did not exceed 7.6 ±0.4 species per plot (Table 2.3, 2.4). Vegetation cover increased significantly with an increase in distance from the shore (Table 2.3, 2.4). Vegetation cover in the upper beach area was highest at closed beaches (52.0 ±2.7 %).

Mean species cover of characteristic plant communities varied significantly among beach types and distances (Table 2.3, 2.4). In general, coverage of species of the Cakiletea maritimae, the Honckenyo-Elymetea and of Ammophiletea arenariae species followed the described sea-to-land gradient. Cakiletea maritimae species exhibited the highest frequency and cover at opened sites in the lower shore area (AB distance a: 33.8 ±5.4 %; Table 2.4). Species of the Honckenyo-Elymetea occurred mainly in closed or partly closed nature conservation areas (Table 2.4). Cover of Ammophiletea arenariae species did not differ between beaches with different accessibility. In accessible beaches, the cover of Artemisietea vulgaris and Molinio-Arrhenatheretea species was significantly highest at sites with a greater distance to the shore (distance e-f). Only the closed conservation area featured an increased cover of Molinio-Arrhenatheretea species in the lower shore area (NSG distance a: 4.4 ±2.3 %).

Table 2.3: The effects of the fixed factors degree of accessibility (use) and distance to the shore (dist) and their interactions on species number, species coverage and plant community classes. In the linear mixed effect model, transect was regarded as random factor. (numDF/denDF: degrees of freedom in the numerator/degrees of freedom in the denomenator)

Response	Factor	numDF/denDF	F	p
Species no.	use	2/134	3.8	0.03
	dist	5/730	35.7	<0.001
	use x dist	10/730	1.8	0.05
Vegetation cover	use	2/134	7.6	<0.001
	dist	5/730	103.2	<0.001
	use x dist	10/730	3.9	<0.001
Cakiletea maritimae	use	2/134	4.8	<0.001
	dist	5/726	1.3	0.3
	use x dist	10/726	6.5	<0.001
Honckenyo-Elymetea	use	2/134	5	<0.01
	dist	5/726	16.6	<0.001
	use x dist	10/726	3.8	<0.001
Ammophiletea arenariae	use	2/134	3.9	<0.05
	dist	5/726	75.6	<0.001
	use x dist	10/726	1.9	<0.05
Koelerio-Corynopheretea	use	2/134	3.5	<0.05
	dist	5/726	3.6	<0.01
	use x dist	10/726	1.6	0.09
Artemisietea vulgaris	use	2/134	1.4	0.04
	dist	5/726	3.1	0.2
	use x dist	10/726	2.7	<0.001
Molinio-Arrhenatheretea	use	2/134	1.8	0.2
	dist	5/726	2.2	0.05
	use x dist	10/726	4.5	<0.001
Others	use	2/134	1.9	0.2
	dist	5/726	4.7	<0.001
	use x dist	10/726	2.1	<0.05

Table 2.4: Vegetation cover, species cover and coverage of main plant community classes (as %) for three levels of beach access assigned into their distances to the shore. Different lower case letters indicate significant differences within the particular distance to the shore derived by multiple contrast tests ($p < 0.05$). (dist: distance to the shore (f: beach ridge; a: 10-12 m from beach ridge; see Figure 2.2); use: degree of beach access (AB: Accessible beach; NSG: Nature conservation area with closed access; NSGH: Partly accessible nature conservation area); sem: Standard error of mean; n.s.: not significant)

Beach access	Distance	Species no.		Vegetation cover		Cakiletea maritimae		Honckenyo-Elymetea		Ammophiletea arenariae		Koelerio-Corynopheretea		Artemisietea vulgaris		Molinio-Arrhenatheretea		Others	
		mean	sem	mean	sem	mean	sem	mean	sem	mean	sem	mean	sem	mean	sem	mean	sem	mean	sem
NSG	a	1.6	0.4 n.s.	7.3	2.1 n.s.	13	4.1 ab	11.6	4.3 ab	2.5	1.4 n.s.	0	0 n.s.	0.2	0.2 n.s.	4.4	2.3 n.s.	6.9	3.1 n.s.
NSGH		1.4	0.3	9.1	2.3	23.3	6.9 a	20.7	6.4 a	0.6	0.6	0	0	0.2	0.2	0	0	3.5	3.4
AB		1.2	0.2	12.2	2.5	33.8	5.4 b	6.5	2.8 b	8.6	3.1	0	0	0	0	0	0	2.4	1.5
NSG	b	1.9	0.3 n.s.	9	1.9 n.s.	7.8	3.5 a	25.7	5.8 ab	8.4	3.4 n.s.	2.7	1.9 n.s.	0.1	0.1 n.s.	3.9	2.4 n.s.	10.6	3.8 n.s.
NSGH		2.2	0.5	14.4	3.4	9	4.8 ab	37.8	8.3 a	3.9	2.2	0	0	0.5	0.4	0.5	0.4	10.3	5
AB		1.9	0.2	6.5	1.4	39.9	5.1 b	13.5	3.7 b	10.1	2.8	0.6	0.1	3.5	1.8	0.7	0.4	2.1	1.5
NSG	c	2.9	0.4 n.s.	20.3	3.3 n.s.	11.4	3.9 n.s.	54.6	6.3 a	14.4	3.9 n.s.	0.2	0.1 ab	0.1	0 n.s.	0.1	0 n.s.	4.9	2.6 n.s.
NSGH		3	0.4	14.8	3.6	18.1	5.4	34.6	6.7 a	9.9	4	0.3	0.3 a	1.2	0.9	0	0	15.2	6.3
AB		3.4	0.4	34.6	1.7	28.5	4.4	17.8	3.7 b	22.5	3.9	2.3	1.1 b	2.1	0.8	4.3	1.9	4	1.7
NSG	d	4.1	0.4 n.s.	34.6	3.1 n.s.	12.2	3.4 n.s.	50.2	5 a	34.2	4.6 n.s.	1.7	0.7 ab	0	0 a	0.1	0 n.s.	1.6	0.5 n.s.
NSGH		5.3	0.4	31.2	3.8	24	5.8	33.3	5.8 a	30.3	5.6	0.4	0.2 a	2.5	1.3 ab	2.3	2	7.1	3.7
AB		5	0.4	24.6	2.7	16.1	3	20.9	3.8 b	35.4	4.2	4.4	1.7 b	8.5	2.1 b	3.7	1.1	5.3	1.5
NSG	e	5.6	0.4 n.s.	52	2.7 a	5.5	2 n.s.	28.9	4.9 ab	60.9	4.9 n.s.	2	0.5 ab	0.4	0.2 a	0.3	0.2 a	1.9	0.8 n.s.
NSGH		7.3	0.5	42.8	3.7 ab	9	3.3	32.6	5.6 a	48.5	5.9	3	1.9 a	1	0.5 a	0.7	0.4 a	4.4	1.2
AB		7.1	0.4	35.2	2.2 b	6.8	1.9	16.4	2.3 b	47.1	3.9	7.3	2.2 b	8.9	1.9 b	7.6	1.7 b	5.7	1.3
NSG	f	7.6	0.4 n.s.	55.2	2.9 n.s.	6.8	1.7 n.s.	14.1	3.6 ab	65	3.7 n.s.	5.3	1.6 ab	1.2	0.3 a	1.2	0.3 a	6.4	1.6 n.s.
NSGH		9.6	0.6	52.3	4.8	1.4	0.5	16.9	3.8 a	60.7	5.6	4.5	2.3 a	3.8	0.9 ab	3.1	1.8 a	7.1	2.2
AB		8.4	0.3	56.2	2.8	1.7	0.4	10.4	1.8 b	52.5	4.3	6.3	1.8 b	12.4	2.3 b	9.4	2.1 b	8.6	1.7

The CCA of the upper shore demonstrated distribution of species being significantly influenced by the distance to the shore (Eigenvalue: 0.21) and accessibility of the beach (Eigenvalue: 0.20; Figure 2.3). Sites with restricted accessibility (NSGH, NSG) showed a smaller distribution of plots, while plots of accessible beaches (AB) had a wide range in the CCA. Species of the Cakiletea maritimae (e.g. *Atriplex glabriuscula, Cakile maritima*) were at the top left of the graph and species of the Ammophiletea arenariae (e.g. *Ammophila arenaria*) at the middle. Non-typical beach species and ruderals were mainly at the right part of the CCA (e.g. *Cirsium vulgare, Poa pratensis, Urtica dioica*).

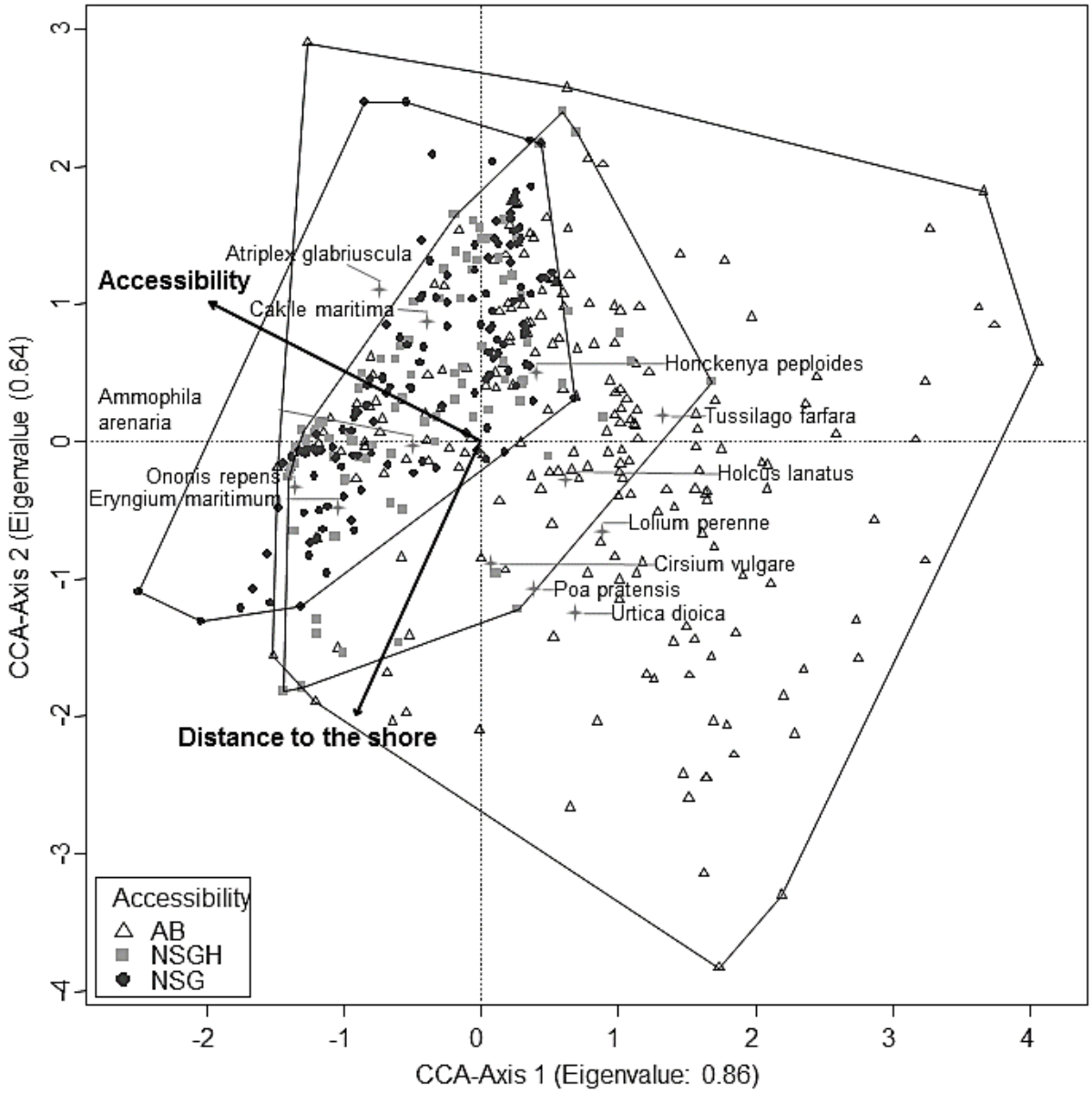

Figure 2.3: Canonical correspondence analysis (CCA) of all vegetated plots of the upper shore (distance d-f) grouped into three types of beach access (AB: Accessible beach; NSG: Nature conservation area with closed access; NSGH: Partly accessible nature conservation area). Degree of accessibility and distance to the shore were chosen as constrained axis (Eigenvalue Accessibility: 0.20; Distance to the shore: 0.21; $p < 0.01$). Several species were added into the graph for better explanation of distribution of plots (position in the CCA was marked with a star).

2.3.2 Response trait patterns

Selected databases characterized 120 plants of our dataset for all traits except root depth, which was assigned for 104 plants. Distribution of all plant traits was influenced significantly by distance to the shoreline and degree of accessibility or its interaction (Figure 2.4, Table 2.5).

All types of beach access contained mostly therophytes in the lower shore and chamaephytes in the upper shore. Partly closed conservation areas (NSGH) featured a significantly higher amount of therophytes at distances d-e than any other type of accessibility ($p < 0.001$; Figure 2.4). This trend was also clearly present for the reproductive trait. The degree of plants with clonal growth showed an increased number of erosulate plants with an increase of distance to the shoreline for all levels of access. Additionally, accessible beaches at the lower shore had greater cover of hemirosette and rosette plants than closed sites (Figure 2.4). Leaf anatomy changed from more plants with succulent leaves at the lower shore to more plants with mesomorph leaves in the upper shore for all types of beach access. Totally closed off beaches and partly closed off beaches had significantly highest occurrences of plants with succulent leaves at the lower shore area (distance a-c; $p < 0.001$; Figure 2.4). Plants with deep roots were significantly increased in totally closed off beaches at the lower shore (NSG). Also, coverage of deep-rooting plants increased with the distance to the shoreline for all types of beach access.

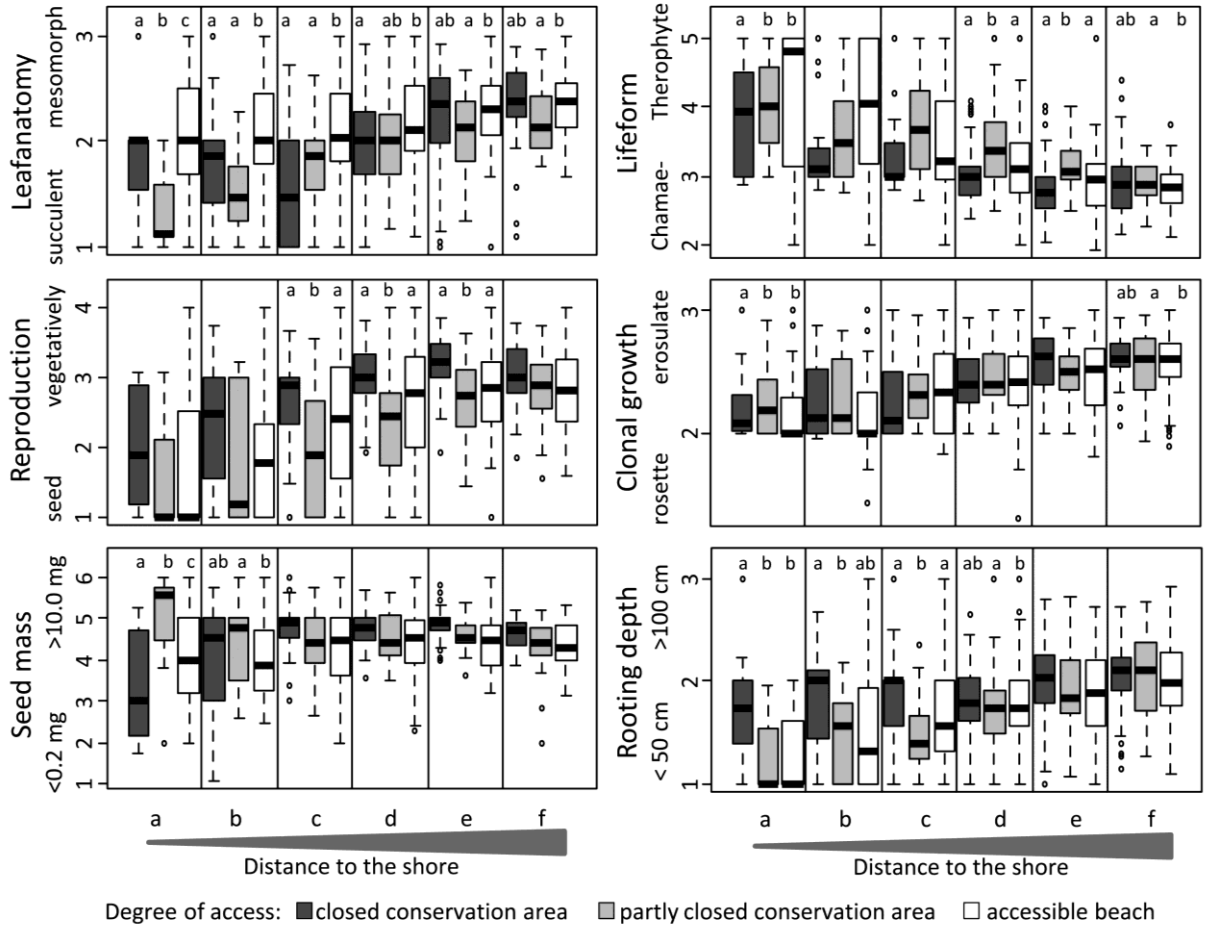

Figure 2.4: Weighted mean values of plant trait classes (leaf anatomy, lifeform, reproduction, clonal growth, seed mass and root depth) according to plots of different types of beach access. Main categories were added on the second axis to explain class values. Lower case letters indicate significant differences between varying levels of beach access in the particular distance to the shoreline ($p < 0.05$). (AB: Accessible; NSG: Nature conservation area with closed access; NSGH: Partly accessible nature conservation area).

Variance of seed mass decreased with an increase in distance to the shore, for all types of beach access. At partly closed conservation areas, significantly more plants with heavy seeds occurred at the lower shore area (a-b; $p < 0.001$) than with any other type of accessibility.

The Spearman rank correlation showed a strong correlation between clonal growth and leaf anatomy ($r=0.67$, $\rho < 0.001$), and correlations between clonal growth and reproduction ($r=0.59$, $\rho < 0.001$), and root depth and reproduction ($r=0.52$, $\rho < 0.001$). Root depth, seed mass and leaf anatomy were not correlated at all.

Table 2.5: The effects of the fixed factors degree of accessibility (use) and distance to the shore (dist) and their interactions on plant traits. In the linear mixed effect model, transect was regarded as random factor. (numDF/denDF: degrees of freedom in the numerator/degrees of freedom in the denomenator)

Response	Factor	numDF/denDF	F	p
Lifeform	use	2/134	1.3	0.3
	dist	5/565	11.3	<0.001
	use x dist	10/565	2.9	<0.05
Clonal growth	use	2/134	3.4	<0.05
	dist	5/565	58.3	<0.001
	use x dist	10/565	4.3	<0.001
Leaf anatomy	use	2/134	70.4	<0.001
	dist	5/565	43.5	<0.001
	use x dist	10/565	17.9	<0.001
Reproduction	use	2/134	1.9	0.16
	dist	5/565	43.6	<0.001
	use x dist	10/565	7.9	<0.001
Rooting depth	use	2/134	26	<0.001
	dist	5/556	33.1	<0.001
	use x dist	10/556	3.4	<0.001
Seed mass	use	2/134	5.9	<0.01
	dist	5/565	8.6	<0.001
	use x dist	10/565	4.1	<0.001

2.4. Discussion

2.4.1 Effects of beach access on plant species richness and composition

The results of this study revealed that species composition, richness and cover vary according to the intensity of interference by beach visitors as well as by the distance from the shoreline.
Vegetation cover barely differed between the degrees of accessibility at the shore, whereas Schierding et al. (2011) revealed that even a low rate of trampling had a negative effect on plant cover compared to no trampling.

Our results showed that a greater species richness at accessible beaches appeared because of the increased amount of non-target generalists or ruderals of the Molinio-Arrhenatheretea (e.g. *Taraxacum officinale*) and the Artemisietea vulgaris (e.g. *Artemisia vulgaris* or *Glechoma hederacea*) in

the upper shore area (Grunewald 2006; Peyrat et al. 2009). At beaches with low human pressure, the number of pioneer annuals and herbaceous foredune plants increased according to Grunewald (2006) and Grunewald and Schubert (2007), while the foredune habitat and the related characteristic species disappeared at beaches with great human pressure (Ciccarelli 2014; Malavasi et al. 2014). An increase in species richness at the shore of our dataset is rather an indicator for intermediate anthropogenic disturbances (Connell 1978). In contrast to this, it was observed that intensive human impact in combination with extreme climatic conditions decreased species richness at sandy coasts (Kutiel et al. 1999; Malavasi et al. 2014).

An increased cover of Molinio-Arrhenatheretea species at the lower shore of closed nature conservation areas in this study is a typical characteristic of drift line areas (Cakiletea maritimae). Drift line plants do not have an actual seed bank in the soil, but rather depend on the sea for regular distribution of seeds along the shore and for the accumulation of drift line material, which serves as nutrient source and enhances soil humidity (Krisch 1990; Garcia-Mora et al. 1999). A great amount of older drift line material accumulate and annual nitrophilous species, which also belong to the Molinio-Arrhenatheretea establish at closed areas (Passarge and Passarge 1973; Krisch 1990; Isermann 2004a). In trampled sites, the decomposition of drift line material is enhanced by disintegration and turbation by trampling.

2.4.2 Effects of beach access on plant traits and ecological functioning

The analysis of characteristic response trait patterns of plant composition revealed an impact of beach access on the shore. The frequency of annuals at the lower shore increased at accessible beaches. The initiation of sand fixation by drift line plants or other annuals might just be temporary, due to their shorter lifespan (Salisbury 1952; Garcia-Mora et al. 1999; Isermann 2004a). Additionally, the cover of plants that reproduce mainly by seeds increased while the cover of plants with great root depth decreased with an increase in beach accessibility. An extensive root system beneath the surface layer supports resistance of above-ground biomass (Salisbury 1952; Garcia-Mora et al. 1999) and stores assimilates that improve the ability of the plant to recover after disturbance (Cornelissen et al. 2003; Puijalon et al. 2008). A loss of deep rooting plants and perennials would lead to a substantial loss of the capacity of sediment fixation and resilience of beach vegetation. Deep rooting plants are long-living, but slowly-growing in their initial phases. Trampling during the initial phases of plant development hinders their establishment at the beach, which was also indicated by the lower coverage of deep rooting plants at the accessible beaches of this study.

At beaches with reduced human access, a greater number of plants with succulent leaves appeared than at public beaches. Garcia-Mora et al. (1999) revealed that leaf succulence and a thick cuticle and epidermis, are important characteristics for perennial beach plants in order to withstand sand burial and aeolian abrasion. Therefore, *Honckenya peploides* is considered to be particularly successful at beaches because of its dense stands, prostrate growth and small leaves. These characteristics disappeared in beach vegetation at accessible sites, indicating a loss of tolerance toward natural disturbances of vegetation (Garcia–Mora et al. 1999; Malavasi et al. 2014).

Sun and Liddle (1993) found erect plants to be less tolerant to human trampling than tussocks and prostrate plants. In our study, however, differences in clonal growth between trampled and conserved sites were less intense because environmental conditions of the beach also promote a

certain degree of clonality at the upper shore (Garcia–Mora et al. 1999). Furthermore, clonal growth was correlated with other plant traits. This indicated that the occurrence of plants with great clonal growth strongly interacted with the suitability of other plant traits (e.g. leaf anatomy and reproduction).

2.4.3 Policy implications for beach management

On one hand, trampling destroys the complex spatial structure and affects main ecological functions of beaches (Labuz and Grunewald 2007; Barbier et al. 2011; Peyrat and Fichtner 2011; Santoro et al. 2012). On the other hand, beach access is essential to coastal tourism and is a prime factor in beach vacation destination (Haller et al. 2011). Thus, beaches closed off for nature conservation interfere with economic interests and become areas of great conflict for stakeholders (Haller et al. 2011).

Beaches are naturally highly resilient ecosystems; they are very tolerant of natural disturbances and are important habitats for a great proportion of pioneer plants, mainly geophytes (Andersen 1995; Garcia-Mora et al. 1999; Lemauviel and Rozé 2003). Studies on formerly accessible sandy coastal areas that were totally closed off showed that vegetation communities can be improved effectively by excluding trampling pressure (Hylgaard 1980; Rozé and Lemauviel 2004; Santoro et al. 2012; Acosta et al. 2013).

A compromise between the demands of nature conservation and tourism are beaches with a minimum of one-third closed upper beach area and accessible lower shore and seawater area (NSGH). Such a management option excludes trampling in areas where naturally perennial plants grow. Trampling at intertidal zones has less impact on beach ecosystems than trampling in upper beach areas and the degree of endangered plants is higher in the upper shore area (Hylgaard 1980; Brown and McLachlan 1990; Andersen 1995; Lemauviel and Rozé 2003; Acosta et al. 2009). According to our results, totally closed and partly closed beaches revealed similar plant species composition but differed significantly in regard to plant traits, leading to negative effects on beach functioning. Thus, partly closed nature conservation areas are a compromise between ecological and tourist needs, but do not replace areas where beach dynamic and ecology are not altered by any anthropogenic interference.

To achieve sustainable beach management, intercommunal spatial planning is required that identifies and protects sensitive beach areas and allows for natural beach dynamics. Despite economic constraints, conservation should aim to reduce direct human pressure on the shore (Kutiel et al. 1999; Grunewald 2006; Ciccarelli 2014). This may be achieved by closing the total shore or at least fencing off the upper shore area. In addition, visitors should be guided by walkways over dunes and boardwalks to concentrate pressure on distinct, small areas (Ciccarelli 2014). Any measures need to be supplemented with conclusive information for visitors and should be developed with a high participation of stakeholders in order to minimize distrust and support acceptance (Defeo et al. 2009; Haller et al. 2011).

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Picture C: **Cakiletea maritimae with mainly *Cakile maritima* growing on buried drift line material.**

Picture D: **The closed off nature conservation area Bottsand with densely growing Ammophiletea areanariae in the upper shore area.**

Chapter 3

Effects of trampling on beach plants at the Baltic Sea

Abstract

In the last century, increases in human population and beach tourism have affected coastlines worldwide. Resulting pressures on beach ecological systems demand research concerning tolerance of beach plants to disturbance by humans.

At three different Baltic Sea beaches, *Atriplex prostrata, Honckenya peploides* and *Crambe maritima* were planted and observed while subjected to trampling stress intensities of 0, 1 and 2 footsteps $m^{-2}d^{-1}$. Plant height, leaf growth, number of leaves, chlorophyll content of leaves, and fitness of photosystem II were measured at monthly intervals. Survival of plants was documented until the following summer. Linear mixed effect models fit the effects of trampling intensity, time and species on growth, photosynthetic productivity and reproduction of plants. Survival was fitted using general linear mixed models for binomial data.

Results indicated that the annual species *A. prostrata* showed an initial decrease in growth at the first trampling treatments, but no effects on seed weight due to trampling pressure. *H. peploides* was not affected by trampling. *C. maritima* had a reduction in growth and survival under any level of trampling pressure. Experimental trampling pressure was compared to observed trampling intensities at beaches with low visitor frequency, which was ascertained to be between 3 and 8 footsteps $m^{-2}d^{-1}$.

Because of the greater potential of endangerment for *C. maritima*, we suggest that nature conservation focus on reducing human trampling on the upper beach area, e.g. by closing this area. This practice would allow tourists continued recreational access to the water as well as to the lower beach area.

3.1 Introduction

Beaches are highly dynamic ecosystems dominated by wind, floods and shifting sediments, which generate a specialised flora and fauna in the transitional zone between land and ocean (Brown and McLachlan 1990; Martinez and Psuty 2004; Defeo and McLachlan 2005; Jędrzejczak 2005; Irmler 2012). Additionally, coasts are of high economic interest leading to worldwide losses of near natural beaches and changes in beach ecology (Liddle 1975; Brown and McLachlan 2002; Schlacher et al. 2007; Defeo et al. 2009). During the last decades, coastal tourism has grown extensively. For 63 % of EU tourists, the coastal areas are the most favoured holiday destinations (EU 1998; Haller et al. 2011). In the Baltic Sea region, tourism is seasonal, concentrating on the warm, dry, summer period from June to August. Forecasts are predicting an extension of the summer season due to climate change, which would increase tourism in this region (EU 2008).

Overuse of beaches and dunes can cause significant damage to vegetation, mainly by destabilization of sandy substrates (Barbier et al. 2011). One main function of beach plants is the reduction of wave and wind energy, and initiation of more sheltered habitats such as primary dunes (Defeo et al. 2009; Barbier et al. 2011; Ellenberg and Leuschner 2012). Consequently, research on disturbance sensitivity of beaches helps to identify ecological beach processes such as dune development, and to understand application of coastal defence by intact beaches (Barbier et al. 2011; Santoro et al. 2012). Therefore, the impact of tourism on the biodiversity of sandy beach ecosystems is a subject of increasing interest in Europe (Jędrzejczak 2004; Davenport and Davenport 2006; Acosta et al. 2009; Santoro et al. 2012).

This study focuses on the direct effects of human trampling on plants. Mechanical stress on plants tends to mobilize assimilates and increase the belowground biomass by allocation of assimilates in storage organs (Fritz et al. 2004; Puijalon et al. 2008). This trade-off not only affects the survival of the plants, but also their reproduction, germination and establishment (Liddle 1975; Fritz et al. 2004). Whereas other studies have shown that trampling reduces plant biomass in greenhouse experiments and destroys belowground organs (Liddle 1973; Boudreau and Faure-Lacroix 2009), our study considers the analysis of human trampling effects under natural conditions in Baltic Sea beaches. Liddle (1975) assumed the force of an average standing man to be 200 g m^{-2}, while dynamic shearing forces of a walking person cause direct downslope displacement of soil and may be up to 32 % of the body weight (Harper et al. 1961; Quinn et al. 1980).

Still, beach vegetation is meant to be highly resistant to disturbance because of its adaptation to natural dynamic environment (Andersen 1995; Garcia-Mora et al. 1999). Thus, it is of particular interest to allow a qualitative assessment of beach plant resistance towards disturbance under natural site conditions. As typical beach species, we chose *Atriplex prostrata, Honckenya peploides* and *Crambe maritima,* each of the three species growing within particular zones at distances from the shoreline. *A. prostrata* is an annual species growing at the lower sandy shore of the Baltic Sea. Here, patchily-occurring sea debris provides the main nutrient source. The perennial succulent *H. peploides* grows at the less wave-washed upper shore. Because of its tiny leaves and dense stands, this species is of importance in sand stabilization (Berg et al. 2004; Labuz and Grunewald 2007). *C. maritima*, a facultative halophytic perennial develops at higher elevated beach ridges at a distance more protected from the sea. This species has broad leaves and a waxy cuticle (Scott 1976). Scott (1976) has proposed that the decrease of *C. maritima* along beaches may be due to trampling by tourists. Consequently, the main research questions of this study are: 1) What effects does human trampling have on growth and photosynthetic productivity of beach species? 2) Do the

beach species differ in their ability to survive trampling? 3) What are the effects of trampling on plant population dynamics?

3.2 Material and method

3.2.1 Trampling intensity

Trampling intensity is often determined as number of passing persons (e.g., Liddle 1991; Andersen 1995). Step length and directness of movement vary between persons; therefore, we determined the trampling intensity as step $m^{-2}d^{-1}$ as analysed by Quinn et al. (1980) and Schierding et al. (2011) in order to enable a comparison between the trampling intensity applied in the experiment to those of accessible but less frequented beaches. Trampling intensities of beach visitors at four infrequently used beaches of the Baltic Sea of northern Germany were measured in 2011 (Stakendorf, Hohenfelde, Behrensdorf, Lippe; Figure 3.1). Beaches were accessible for visitors, but infrequently used because of secluded location and only a few nearby tourist accommodations such as parking lots, toilets or shops. At each beach, seven plots were built by flattening a sandy area of 4 m^2 at a distance of 8 m to the current shoreline and were marked with stones and GPS tracking points. Plots were not recognizable by beach visitors. Number of footsteps was counted four times; each counting was preceded by a period of 48 hours. Data were not collected during rain to minimise bias. The measured trampling intensity at the four beaches was highest at Hohenfelde (7.78 ±1.32 steps $m^{-2}d^{-1}$) and significantly lowest at Stakendorf (3.60 ±0.44 steps $m^{-2}d^{-1}$; Figure 3.2).

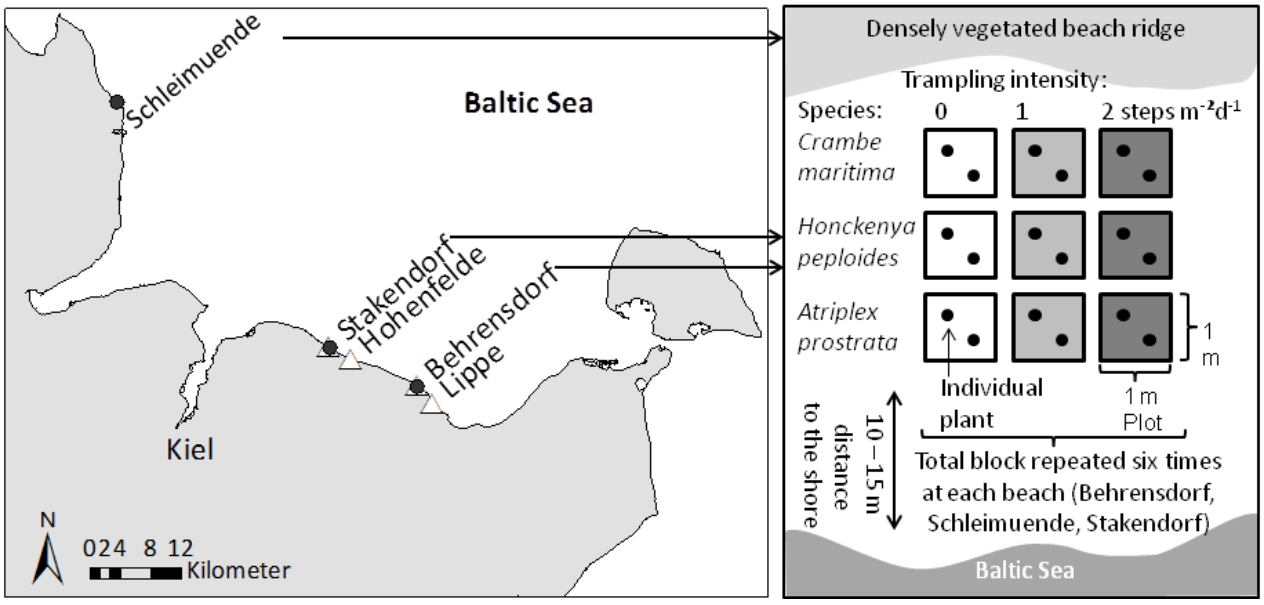

Figure 3.1: Study design and map of the experimental sites along the Baltic Sea. Dark circles (●): experimental areas. White triangles (Δ): survey areas of trampling intensity at less intensively used beaches.

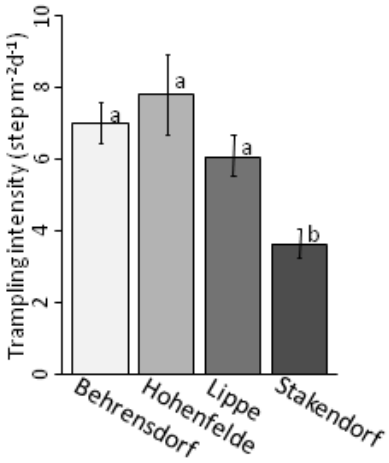

Figure 3.2: Trampling intensity at less intensively-used beaches at the Baltic Sea, measured at four days in summer, 2011. Lower case letters indicate significant differences ($p < 0.05$).

3.2.2 Plant material

Seeds of *A. prostrata, H. peploides* and *C. maritima,* were collected in 2011 near the experimental sites. Plants were bred in the Botanical Garden at the Kiel University. To induce germination, testae of *A. prostrata* and of *C. maritima* seeds were removed. All seeds were treated with 1 g l^{-1} gibberlic acid. Additionally, seeds of *C. maritima* were stratified at 2-5 °C in sand for one month to induce germination. All seeds were sown in the greenhouse at 18 °C in soils with high humus content in mid March, 2012. After germination, plants were brought to the field area of the Botanical Garden to adapt to near-natural climate conditions. All plants were planted on the 5th, 6th and 12th of May at Stakendorf (STA), Behrensdorf (BSD) and in Schleimuende (SCH), respectively (Figure 3.1, Table 3.1).

3.2.3 Experimental design

The experiment was conducted in conservation areas on the three beaches from May, 2012, to June, 2013. Stakendorf (STA), Behrensdorf (BSD) and Schleimuende (SCH) were chosen as experimental areas, because they represent the mean biotic and abiotic conditions at southern Baltic Sea beaches with greater sand content (Table 3.1). Naturally, all examined species were found in the direct vicinity of the experimental areas. Usually, tourist access is partially (BSD, STA) or totally (SCH) restricted in these areas and beach wrack material is not removed. The experimental areas were placed in 10 to 15 m distances to mean water level. Each beach site consisted of six blocks, each containing nine plots. Three plots were equipped with two plants of one species. Each species was treated with loads of 0, 1 and 2 footsteps $m^{-2}d^{-1}$ (Figure 3.1). The experiment was protected by a six-corner-mesh-fence to prevent disturbance from rabbits, and accidental trampling by people and animals. The plants were watered regularly for the first week to promote successful establishment. In June, 2012, after an adaptation period of four weeks, treatment with different disturbance intensities was begun and ended in October, 2012. Controlled human trampling was conducted regularly by a person randomly stepping on each 1 m^2 plot with intensities of 0, 1 and 2 footsteps $m^{-2}d^{-1}$. By using humans walking on plants rather than simulation by dropping weights, we took also the shearing effect into account (Quinn et al. 1980).

3.2.4 Environmental measurements

Soil texture, net soil level changes and events of flooding were documented at the experimental sites. Soil conditions were assessed according to Schlichting et al. (1995) at each site in twelve randomly distributed 1 m² plots. Net soil level changes were measured using ten erosion pins of 1 m length (5 mm diameter; Haigh 1977) buried up to half their length. The pins were dispensed next to the plots in each row of the experimental area and measured three times a week during the treatment in 2012. Flooding events were detected using cups which were protected from rainwater and buried in the ground.

Soil texture showed an increased amount of large round stones in BSD in contrast to the other sites (Table 3.1). Nevertheless, all sites consisted of at least 70 % sand. Net soil level changes differed at the individual beaches, but never exceeded 4 cm from May until mid of September, 2012 (Table 3.1).

Table 3.1: Site conditions at the three experimental areas Behrensdorf, Schleimuende and Stakendorf.

Beach site		Behrensdorf	Schleimuende	Stakendorf
Abbreviation		BSD	SCH	STA
Coordinates		N 54° 21.158792 E 10° 37.084831	N 54° 41.702873 E 10° 1.548402	N 54° 24.130980 E 10° 26.748460
Conservation status		closed upper beach area	closed	closed upper beach area
Beach width		14-20 m	10-17 m	20-28 m
Soil texture	stones	11.8 ±3.5 %	1.1 ±0.7 %	2.5 ±0.8 %
	gravel	4.3 ±2.1 %	5.2 ±1.6 %	1.7 ±1.7 %
	sand	72.5 ±5.4 %	82.9 ±2.9 %	78.8 ±3.8 %
Net soil level changes		-0.13 ±0.06 cm	-0.05 ±0.06 cm	-0.13 ±0.06 cm

3.2.5 Plant measurements

All individuals were measured once at the beginning of the treatment in June, 2012, and then at four week intervals, and once again a year later in June, 2013. To assure longer observation, all measuring methods were chosen to be non-destructive (Andersone et al. 2011):

1) Growth was recorded documenting total height, number of leaves and length of leaves. For *A. prostrata* and *H. peploides,* lengths of ten leaves were measured; for *C. maritima,* lengths of all leaves were measured. Dead leaves were not counted or measured.

2) Photosynthetic productivity was measured, analyzing the chlorophyll content of leaves optically using a chlorophyll content meter (CCM-200, Opti-Sciences, Tyngsboro). To verify accuracy of these optical measurements, we compared optically determined chlorophyll content of ten leaves to their extracted chlorophyll a+b content. Since the method is destructive, leaves were taken from plants growing next to the experiment. Chlorophyll was extracted from leaf discs of 10 mm diameter with 1.5 ml buffered 80 % aqueous acetone. The spectrum (between 750 and 600 nm) was recorded by a photometer (Uvikon 922 spectrophotometer, Kontron-Instruments, Zurich) and chlorophyll a+b content was calculated regarding Porra et al. (1989). Finally, relative

optical results of the experiment where compared to the calibration curve of optically-measured relative chlorophyll values and extracted absolute chlorophyll values.
The fitness of the photosystem II (PSII) was determined by using a portable pulse amplitude modulated chlorophyll fluorometer (Mini-PAM, Heinz Walz GmbH, Effeltrich, Germany). At midday and early afternoon, parts of leaves were covered for 20 minutes with metal leaf clips to measure the minimal fluorescence (F0) by using a pulse-modulated measuring light of 0.12 mmol photons $m^{-2}s^{-1}$ at a frequency of 0.6 kHz. The maximal fluorescence (Fm) was measured by a 1 s saturating light pulse at about 10 000 mmol photons m^{-2} s^{-1}. The maximum PSII photochemical efficiency was determined as Fv/Fm, where Fv is defined as the variable fluorescence in the dark-adapted state (Fv=Fm-F0). It was not possible to conduct any optical measurements for determination of photosynthetic productivity on *H. peploides,* because of the small leaf size.

3) Reproduction was determined after flowering and seed production of *A. prostrata.* Seed samples were collected in August, 2012. Bracts were carefully removed from the seeds and seeds were dried for 72 hours at 60 °C, and weighed using a scale directly afterward in groups of five seeds.

4) Plant survival was documented at each measuring point until June, 2013.

3.2.6 Data analysis

All data from June until beginning of September regarding biomass and photosynthetic productivity were taken as relative values. The values of the first measuring point before the beginning of the treatment in June were taken as 100 %. All data were evaluated using R, version 2.10.1 (R 2012). The data were assumed to be normally distributed and to be heteroscedastic due to the different levels of beach site, species and time, based on graphical residual analysis of each model. Statistical linear mixed effects models were used to evaluate the data of changes in plant height, number of leaves and leaf length (Laird and Ware 1982; Verbeke and Molenberghs 2000). The statistical model included species (*A. maritima*, *H. peploides* and *C. maritima*), trampling intensity (0, 1 and 2 footsteps $m^{-2}d^{-1}$) and time (measurements every four weeks in July, August and September), as well as all their interaction terms (two-fold and three-fold) as fixed factors.

Further statistical linear mixed effects models were used to evaluate the data of fitness of photosystem II and chlorophyll content. The statistical model included species (*A. maritima* and *C. maritima*), trampling (0, 1 and 2 footsteps $m^{-2}d^{-1}$) and time (measurements every four weeks, three times over a 12 week period), as well as all their interaction terms (two-fold and three-fold) as fixed factors.

For all five models, the beach site (BSD, SCH and STA), block (1-6), and plot, each nested, were regarded as random factors. Also, the correlations of the measurement values of the several levels of time were taken into account using an auto-regressive correlation structure for the residuals of the order 1 (AR-1). This structure represents a decline in temporal correlation for increasing lags or number of months between observations (Pinheiro and Bates 2009).

A statistical linear mixed effects model was used to evaluate the data of seed weight of *A. prostrata*. The data were assumed to be normally distributed and to be heteroscedastic due to the different levels of beach site and trampling intensity, based on a graphical residual analysis. The statistical

model included trampling (0, 1 and 2 footsteps $m^{-2}d^{-1}$) as fixed factor. The beach site (BSD, SCH and STA), block (1-6), and plot, each nested, were regarded as random factors.

The analysis of the binomial data of the survival of plants started with the definition of a logistic regression using a generalized linear mixed model with the logit-link. The statistical model included species, trampling and time (six times measured at 0, 4, 8, 12, 16, and 52 weeks) as well as all their interaction terms as fixed factors. The beach site (BSD, SCH and STA), block (1-6), and plot, each nested, were regarded as random factors. Also, the correlations of the measurement values due to the several levels of weeks (time) were taken into account.

For each model an analysis of variances (ANOVA) was conducted to evaluate the influence of fixed factors. After this, multiple contrast tests (Bretz et al. 2011) were carried out in order to compare the several levels of the influence factors, respectively.

3.3 Results

3.3.1 Plant biomass

The influence of trampling intensity, time and species differed between the response parameters for biomass (Figure 3.3).

Changes in plant height differed according to trampling intensity, species and time (Table 3.2). *A. prostrata* showed a decrease in changes in plant height due to increased trampling intensity in July and a strong tendency in August. Mean plant height in July was 9.4 ±1.0 cm for non-trampled and 6.5 ±1.0 cm for plants treated with 2 steps $m^{-2}d^{-1}$ or 260.4 ±40.8 % and 165.3±41.1 % changes in plant height, respectively (Figure 3.3). Greatest plant heights of *A. prostrata* were reached in August with a maximal height of 47.5 cm. *C. maritima* and *H. peploides* did not grow as high as specimens of *A. prostrata* at all and did not show any significant effect of trampling intensity. *C. maritima* grew maximally 18.2 cm high and *H. peploides* 15.0 cm. Plant height in *C. maritima* maximally doubled until September, e.g. in September changes in plant height for non-trampled individuals were 204.3 ±43.5 % (Figure 3.3). Plant height of *H. peploides* mainly decreased during the experiment, and mean changes of plant height ranged between 59.3 % and maximally 107.3 %.

Changes in leaf length differed due to different levels of trampling intensity, species and time (Table 3.2). *A. prostrata* showed significant decrease of leaf length due to higher levels of trampling intensity in July, whereas *C. maritima* showed a decrease of changes in leaf length due to trampling in September. Maximal leaf length of *A. prostrata* was 8.5 cm at the beginning of the experiment in June. In July, leaves of non-trampled individuals increased up to 112.5 ±17.4 %, whereas leaves treated with 2 steps $m^{-2}d^{-1}$ decreased to 89.2 ±17.5 % within the same time period (Figure 3.3). Length of leaves of *C. maritima* increased from a maximal length of 5.7 cm in June to maximally 30.9 cm in September. Individuals treated with 2 steps $m^{-2}d^{-1}$ increased maximal leaf length to 16.9 cm in September. Changes of leaf length in September compared to June were 204.7 ±24.0 % for non-trampled and 106.5 ±23.0 % for individuals treated with 2 steps $m^{-2}d^{-1}$ (Figure 3.3). *H. peploides* did not show any significant changes in leaf length with different levels of time and treatment. Mean leaf length ranged between 1.0 cm and 0.3 cm.

Changes in number of leaves differed significantly due to different levels of species and time (Table 3.2). *H. peploides* showed greatest reduction in number of leaves of all species. In July mean changes in leaf number were 296.4 ±86.0 % for non-trampled individuals and 207.8 ±86.0 % for plants

treated with 2 steps $m^{-2}d^{-1}$ (Figure 3.3). Changes in number of leaves reduced to 48.5 ±32.3 % for non-trampled individuals and 5.0 ±33.4 % for plants treated with 2 steps $m^{-2}d^{-1}$ in September. *C. maritima* had least changes in number of leaves, which ranged between 101.9 % and 192.0 %. Absolute number of leaves of *C. maritima* was between 1 and 14 of all examined individuals. In August, *A. prostrata* had a great increase in number of leaves, up to 457.6 ±67.5 % (114.9 ±15.4 absolute numbers of leaves) for non-trampled and 328.2 ±69.3 % (72.4 ±15.2 absolute numbers of leaves) for plants treated with 2 steps $m^{-2}d^{-1}$ (Figure 3.3).

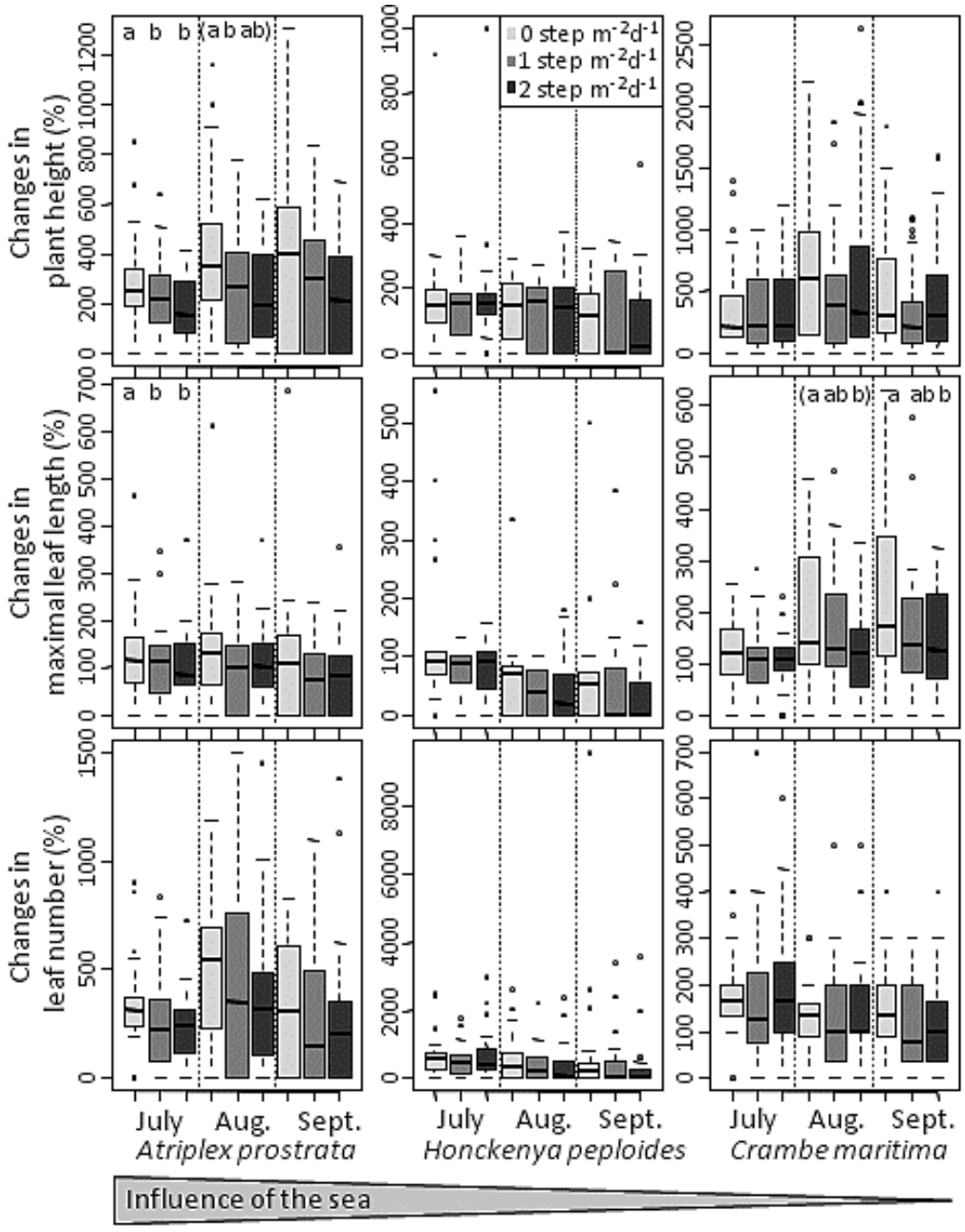

Figure 3.3: Changes of plant growth (plant height, maximal leaf length and number of leaves) of *Atriplex prostrata*, *Honckenya peploides* and *Crambe maritima* at different intensities of simulated low trampling pressures (light grey: no steps; grey: 1 step $m^{-2}d^{-1;}$ dark grey: 2 steps $m^{-2}d^{-1}$) at three measurement periods compared to plant growth before the beginning of the experiment in June (100 %). Lower case letters indicate significant differences ($p < 0.05$) and tendency (placed in brackets: $p < 0.10$) due to different levels of trampling intensity.

3.3.2 Photosynthetic productivity

Fv/Fm ranged between 0.60 and 0.82 at the first measurement period before the beginning of the treatment. Neither trampling nor species or time showed any significant effects on changes in Fv/Fm (Figure 3.4, Table 3.2). At the end of the experiment, changes in Fv/Fm were 72.8 ±9.5 % for 2 footsteps $m^{-2}d^{-1}$ and 89.6 ±9.3 % for non-trampled individuals of *A. prostrata*. For *C. maritima*, changes of Fv/Fm were less intense with 97.3 ±10.9 % for 2 footsteps $m^{-2}d^{-1}$ and 98.1 ±10.1 % for non-trampled individuals in September, compared to values of Fv/Fm at the beginning of the experiment (Figure 3.4).

Although obvious trends in the data, no significant changes in chlorophyll content of *A. prostrata* and *C. maritima* were observed for different levels of trampling intensity (Figure 3.4, Table 3.2). Mean chlorophyll a+b content of *A. prostrata* was 23.9 % to 24.9 % at the beginning of the experiment. In September, lowest chlorophyll a+b content was achieved with 18.3 ±2.6 % for individuals treated with 2 steps $m^{-2}d^{-1}$. The decrease of chlorophyll a+b content over time was significant for non-trampled *A. prostrata*. Absolute chlorophyll content of *C. maritima* was higher than values of *A. prostrata*. Greatest chlorophyll a+b content of *C. maritima* at all was 62.6 %. Greatest mean value was achieved at the end of the experiment for non-trampled individuals with 35.4 ±2.2 %. In September, lowest values for chlorophyll a+b were achieved with 28.6 % for individuals treated with 2 footsteps $m^{-2}d^{-1}$. Nevertheless, changes in chlorophyll a+b content of *C. maritima* stayed rather stable between 114.0 ±7.2 % and 92.2 ±7.6 % of the values of the first measurement period before the beginning of the treatment (Figure 3.4).

3.3.3 Reproduction ability

Seed weight of *A. prostrata* did not show any significant impact of trampling intensity (Table 3.2). Mean seed weight of *A. prostrata* with no trampling treatment was 0.89 ±0.14 mg, whereas the treatment of 2 steps m^2d^{-1} had a seed mass of 0.56 ±0.10 mg. Trampling treatment of 1 steps m^2d^{-1} resulted in a mean seed weight of 0.79 ±0.15 mg.

One year after treatment, the flowering of three individuals of *C. maritima* was documented at the site BSD. One plant was previously trampled with an intensity of 2 steps $m^{-2}d^{-1}$ and two were not trampled. Because of the low number of flowering individuals, seed weight was not documented.

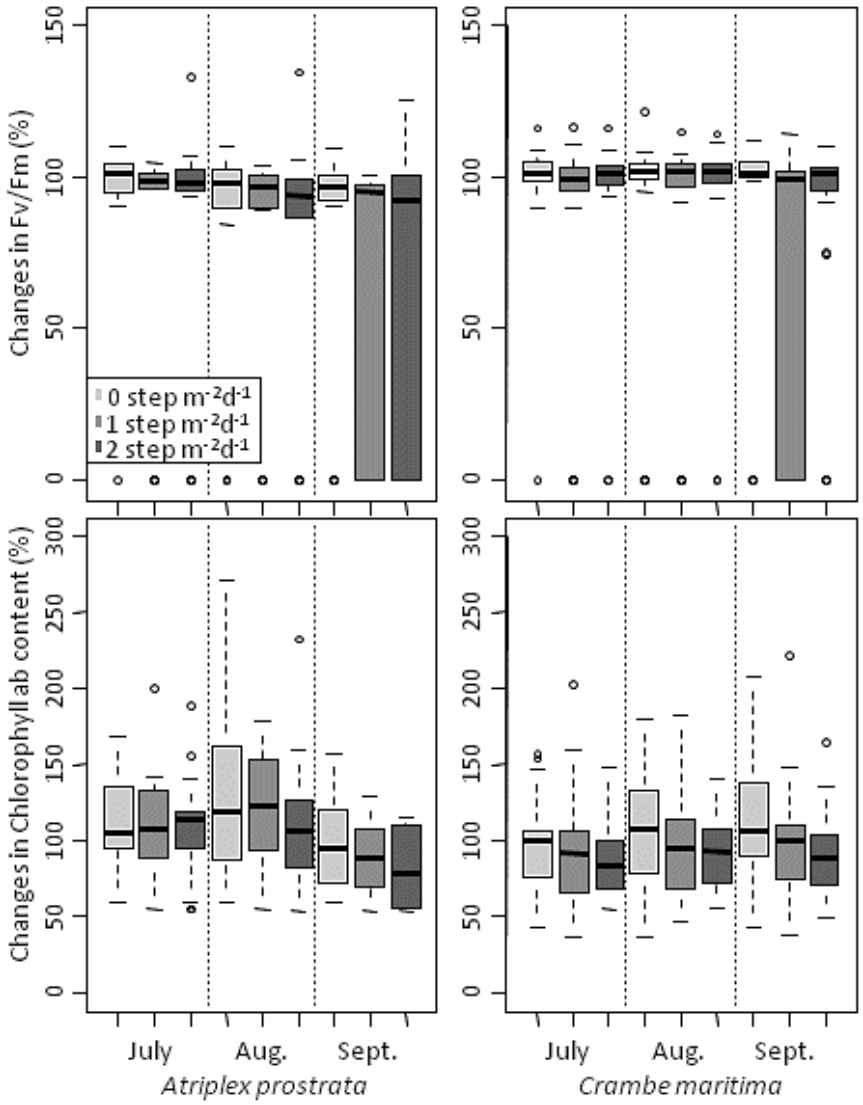

Figure 3.4: Changes of plant photosynthetic productivity (fitness of the photosystem II and chlorophyll a+b content) of *Atriplex prostrata* and *Crambe maritima* at different intensities of simulated low trampling pressures (light grey: no steps; grey: 1 step $m^{-2}d^{-1;}$ dark grey: 2 steps $m^{-2}d^{-1}$) at three measurement periods compared to plant growth before the beginning of the experiment.

Table 3.2: The impact of the fixed effects trampling intensity, species and time on the response variables for biomass, photosynthetic productivity, survival and reproduction. F- and p- values were derived from appropriate statistical linear mixed effect models including the beach site, block and plot, each nested as random factors. The correlations of the measurement values due to the several levels of time were taken into account using an auto-regressive correlation structure.

Response		Fixed effects	num / den DF	F	p
Biomass	Changes in maximal height	Trampling	2 / 126	4.4	
		Species	2 / 126	18.0	<0.0001
		Time	3 / 625	12.9	<0.0001
		Trampling : Species	4 / 126	1.6	0.17
		Trampling : Time	6 / 625	1.3	0.27
		Species : Time	6 / 625	4.0	0.003
		Trampling : Species : Time	12 / 625	0.7	0.65
	Changes in maximal leaf length	Trampling	2 / 127	1.6	0.20
		Species	2 / 127	8.8	0.0003
		Time	3 / 630	5.4	0.005
		Trampling : Species	4 / 127	0.9	0.49
		Trampling : Time	6 / 630	0.6	0.66
		Species : Time	6 / 630	10.7	<.0001
		Trampling : Species : Time	12 / 630	3.1	0.002
	Changes in leaf number	Trampling	2 / 126	0.6	0.53
		Species	2 / 126	4.7	0.01
		Time	3 / 625	8.6	0.0002
		Trampling : Species	4 / 126	0.7	0.58
		Trampling : Time	6 / 625	1.3	0.28
		Species : Time	6 / 625	9.5	<0.0001
		Trampling : Species : Time	12 / 625	0.6	0.79
Photosynthetic productivity	Changes in Fitness of PS II (Fv/Fm)	Trampling	2 / 64	1.1	0.33
		Species	1 / 64	0.1	0.79
		Time	3 / 313	1.2	0.31
		Trampling : Species	2 / 64	0.4	0.68
		Trampling : Time	6 / 313	0.1	0.99
		Species : Time	3 / 313	0.3	0.71
		Trampling : Species : Time	6 / 313	0.3	0.90
	Changes in Chlorophyll a+b content	Trampling	2 / 73	0.5	0.61
		Species	1 / 73	4.9	0.03
		Time	3 / 312	9.1	0.0001
		Trampling : Species	2 / 73	0.3	0.74
		Trampling : Time	6 / 312	1.1	0.36
		Species : Time	3 / 312	11.5	<0.0001
		Trampling : Species : Time	6 / 312	0.9	0.49
Reproduction	Seed weight	Trampling	1 / 33	1.2	0.31

3.3.4 Survival

Low intensive trampling did not influence survival of *A. prostrata* and *H. peploides* significantly, but did affect survival of *C. maritima* (Figure 3.5). Plant survival of trampled *C. maritima* significantly differed after 16 weeks of treatment. In June 2013, 38.9 % treated with 1 step $m^{-2}d^{-1}$ (30.6 % 2 steps $m^{-2}d^{-1}$) of individuals survived in comparison to non-trampled *C. maritima* with an overall survival of 78.8 %.

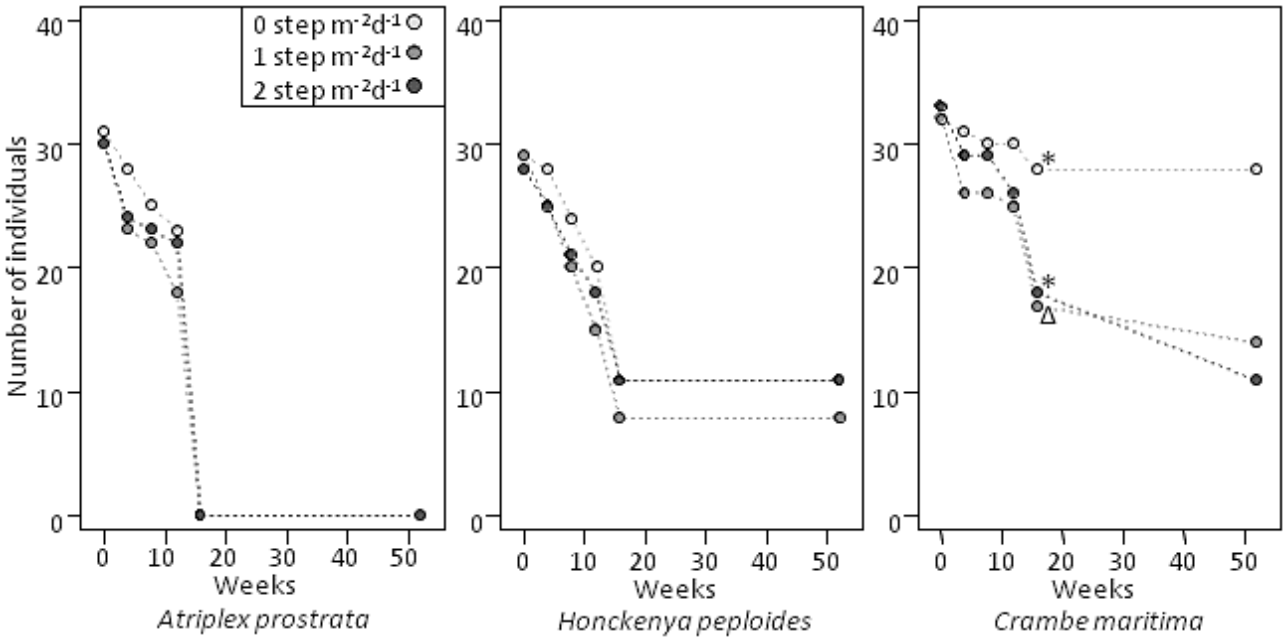

Figure 3.5: Survival indicated as number of individuals of *Atriplex prostrata, Honckenya peploides* and *Crambe maritima* from June 2012 until June 2013. (*: significant difference between levels of trampling intensity at this measuring point ($p < 0.05$); Δ: tendency of difference between different levels of trampling intensity at this measuring point ($p < 0.10$))

3.4. Discussion

3.4.1 Trampling effects on plant growth and photosynthetic productivity

In beach ecosystems, plants reduce wave and wind energy (Defeo et al. 2009; Barbier et al. 2011; Ellenberg and Leuschner 2012), which initiates the development of primary dunes and beach ridges. Therefore, plants serve functions of habitat and biodiversity by creating less stressful habitats where less robust plants can establish. Previous studies have shown the ability of drift line plants such as *A. prostrata* to adapt to changing and unfavourable conditions such as sand burial and poor nutrient supply (Lee and Ignaciuk 1985; Gilbert et al. 2008), or salt stress (Lee and Ignaciuk 1985; Woodell 1985). Gilbert et al. (2008) stated that, under sufficient nutrient supply, "mobile-dune species" achieve high production rates to compensate for loss of biomass due to sand burial. Nevertheless, trampling activity by beach visitors was determined to be more harmful for plant development than natural stress (Santoro et al. 2012), decreasing the diversification of plant populations at beaches (Puijalon et al. 2008) and finally hindering a prolonged dune development substantially (Hesp et al. 2010; Barbier et al. 2011).

The examined beach plants indicated different resistances to trampling according to their relative biomass. In our study, at the beginning of the experiment in July, *A. prostrata* showed a strong decrease in biomass growth relative to trampling. In contrast to *A. prostrata,* trampling effects on maximal leaf length in *C. maritima* increased with time within the first year of establishment at the beach. *C. maritima* is not restricted to the drift line but occurs on the elevated beach area (Berg et al. 2004). Additionally, trampling effects may be caused by root damage and increased soil movement at the roots due to trampling. Boudreau and Faure-Lacroix (2009) observed a significant reduction of below-ground biomass even on the wiry roots of *Leymus mollis*, while no significant reduction of above-ground biomass was observed. *A. prostrata* is an annual species which might lead to less intense trampling effects at the roots.

Sun and Liddle (1993) described that woody, erect plants are less tolerant to trampling than tussocks and prostrate plants, which have more tolerance due to flexibility and tensile strength as well as through avoidance of mechanical impact. In addition, the resistance of plants to trampling is greatly influenced by leaf width and leaf growth. *C. maritima,* which has broad leaves of 2 to 50 cm length (Scott and Randall 1976), is less tolerant of physical stress than *H. peploides*, which has small leaves and prostrate growth characteristics (Liddle 1991). *C. maritima* also has a thick waxy cuticle (Scott and Randall 1976) which can be severely damaged by pressure and shearing forces. This would lead to water stress in the leaf and to partial withering of the leaf tissue.

The photosynthetic efficiency of plants is directly affected by the decrease of chlorophyll content, which may be caused by either a decline of leaf thickness or a lesser number of chloroplasts (Björkman 1981; Murchie and Horton 1997). Less carbon allocation within the process of re-growth of lost plant material may induce a decline in photosynthetic capacity and chlorophyll content. Furthermore, severed vasculature indirectly affects photosynthetic activity, due to stomata closure and reduced CO_2 assimilation to prevent water loss at disrupted leaf tissues (Schmidt 2009). Additionally, damage of plant tissue due to trampling may also induce senescence processes. These processes cause the mobilization of nitrogen and minerals, disassembly of the photosynthetic apparatus, and direct alteration of photosynthetic activity (Lu et al. 2001; Fritz et al. 2004; Puijalon et al. 2008). However, in our experiment, chlorophyll content showed no explicit significant reduction due to trampling. Observed tendency of reduced fitness of PSII and significant reduction in chlorophyll a+b content over the short time in the annual plant *A. prostrata* may rather be due to natural senescence processes. Gilbert et al. (2008) observed that buried dune plants prefer to replace photosynthetic leaf area by producing new leaves rather than changing photosynthetic rate. This indicates that indirect damage might be more critical than direct damage, as long as an essential nutrient source is provided, by sea debris, for example.

3.4.2 Effects on population dynamics

Trampling directly influences plants by damaging plant organs (Sun and Liddle 1993) and changing vegetation cover (Hylgaard 1980; Andersen 1995; Defeo et al. 2009), and indirectly affects them by altering soil conditions (Liddle 1975; Quinn et al. 1980). Our study indicated that some plants already showed an initial decrease in plant growth (*A. prostrata*) and others a reduction in plant growth and plant survival (*C. maritima*) even with very low trampling pressure. Actual trampling pressure of less intensively frequented beaches was about four times higher than in the experiment. Consequently, effects of effective trampling pressure are estimated to be intense and

destructive for plant populations, even among beach plants adapted to robust site conditions. Scott (1976) proposed that human trampling is the main reason for the loss of *C. maritima* at the British coast. Our data underlined the low tolerance towards trampling on the survival of *C. maritima*. In winter, *C. maritima* as a hemicryptophyte stores nutrients in its roots so that below ground organs survive during winter (Scott and Randall 1976). The permanent damage of roots by trampling during summer leads to a reduction in biomass allocation in the roots. Vegetation analyses in trampled dunes and fore-dunes showed a decrease in vegetation cover and an increase in more annuals and trampling-tolerant ruderal and grassy species (Andersen 1995; Garcia-Mora et al. 1999; Labuz and Grunewald 2007; Seer et al. in prep.). Populations of *A. prostrata* may be less affected by trampling; they showed recovery after an initial period of biomass loss. As an annual plant, production of seeds is its main vector of population survival and plant dispersal (Garcia-Mora et al. 1999). The removal of debris may be a main reason for the loss of annual drift line plants at the shore. Seeds of these plants usually accumulate in sea debris for germination (Jedrzejczak 2005; Labuz and Grunewald 2007; Mossbauer et al. 2012).

3.4.3 Further ideas for sustainable beach management

Research on the exclusion of human trampling in primary dunes and older dune systems showed a promising recovery of vegetation density and species diversity, even in a considerably short time period (1 year: Hylgaard 1980; 1-2 years: Santoro et al. 2012). These findings encourage ideas of sustainable beach management that focus on thoughtful coastal spatial planning for areas of tourist use as well as for sensitive beach areas closed for reasons of nature conservation (Defeo et al. 2009; Barbier et al. 2011; McLachlan et al. 2013). The focus of conservation should aim on reducing direct human pressure at beaches (Barbier et al. 2011, Santoro et al. 2012). Closing the total beach or at least fencing the upper beach area is a usual measure. Limiting tourist access to the upper shore parallel to the coastline might already be sufficient to support near natural vegetation cover and promote the main beach functions. This would especially protect habitable zones for *C. maritima* which revealed a high endangerment potential in this study. Moreover, a worldwide analysis from Brown and McLachlan (1990) on disturbance sensitivity of coastlines has shown that particularly the upper shore area and young primary dunes are the most sensitive areas in the coastal sequence. Partly fenced beaches would allow tourists to access the water and use the lower beach area for recreation. Beaches totally closed for reasons of nature conservation interfere with economic interests, because beach access is the prime factor in beach vacation destiny (Jędrzejczak 2004; Haller et al. 2011). Additionally, visitors should be guided by walkways over dunes and boardwalks at the shore to concentrate pressure on distinct areas. All measures need to be supplemented with explanatory information for visitors and should be developed with a high participation of stakeholders in order to minimise distrust and support acceptance (Defeo et al. 2009; Haller et al. 2011).

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Picture E: ***Crambe maritima*** **at the beach of Hohenfelde.**

Picture F: ***Honckenya peploides*** **in the conservation area „Kleiner Binnensee bei Behrensdorf“.**

Chapter 4

How much space is needed for spider conservation? Home range and movement patterns of wolf spiders (Aranea, Lycosidae) at Baltic Sea beaches

Abstract

Beaches are often intensively used by tourists that compete with the area demands of specialised species. In order to estimate the area demand of beach spiders, home range, distribution and population dynamics of three species of Lycosidae (*Arctosa cinerea, Arctosa perita* and *Pardosa agricola*) were observed by mark-recapture experiments at two closed nature conservation beach areas at the Baltic Sea. Results revealed that the home range size of *A. cinerea* varied between beaches. The size of minimal complex polygons of males at a narrow sandy beach was 143.18 ±22.62 m² (females: 164.70 ±13.48 m²) and was so significantly smaller than those found at a broader beach (males: 182.60 ±13.46 m²; females: 179.36 ±47.89 m²) with about 12 % stone coverage. General distribution of all spiders showed an increased frequency on the upper beach area. Estimates on the population size of the three species during summer revealed the highest population size in May and the least at the end of July.

In addition, movement behaviour of *A. cinerea* was observed at a nature conservation area and at an accessible beach. Direct observations of movement patterns indicated that disturbed spiders take more detours and focus their movements seaward where they will be confronted with non-suitable conditions. This study underlines the sensitivity of predatory arthropods of beach habitats to human disturbance. This is particularly critical for the upper beach area. Based on these results, means of achieving viable arthropod populations through adjusted beach management are derived.

4.1. Introduction

Coastlines are dynamic ecosystems where regular flooding, wave movements and wind create harsh habitat conditions with a strong sea-to-land gradient (Brown and McLachlan 1990; Martinez and Putsy 2004). Variability in the distribution, composition and structure of sandy beach arthropod communities has already been linked to differences in the environment and to beach morphodynamics (Schierding et al. 2011). Because of the high recreational value of the sea, beach visitors expose this zone to regular and intensive disturbances (Barbier et al. 2011; Haller et al. 2011). Intensive beach use by tourists leads to a reduction of vegetation, changes animal communities and alters beach ecology worldwide (Liddle 1975; Llewllyn and Shackley 1996; Brown and McLachlan 2002; Schlacher et al. 2007; Bonte and Maes 2008; Defeo et al. 2009; Schierding et al. 2011; Dugan et al. 2012). This poses the challenge of developing beaches with a functioning ecology despite the pressure of tourism (Schlacher et al. 2007; Defeo et al. 2009; Dugan et al. 2012). Presently, conservation areas primarily take birds into consideration by protecting breeding zones or nesting areas for migration (Veloso et al. 2008). Movement, utilization and population data are essential for understanding ecological processes at different trophic levels and, in particular, understanding habitat requirements of coastal arthropods (Samietz and Berger 1997). Thus, the effects of habitat management on sandhopper, insect and spider distribution have been investigated in several studies (Wę slawski et al. 2000; Vahder and Irmler 2010; Schierding et al. 2011; Irmler 2012; Schierding et al. 2013). In general, the movement behaviour of animals is driven by essential needs such as food, mating, breeding, avoidance of predation and avoidance of unfavourable physical and seasonal conditions (Kraus and Morse 2005; Ahrens and Kraus 2007). Thus, species abundance as well as behavioural change due to human disturbance may indicate the impact of humans on arthropod population and ecosystem functioning (Sutherland 1996). Beaches are inhabited by several predatory arthropods such as Carabidae (Schierding et al. 2011), Staphylinidae (Irmler 2012) and Araneae (Schultz and Finch 1990; Vahder and Irmler 2010), which mainly feed on marine arthropods such as Gammaridae or terrestrial Diptera. They, in turn, serve as a food source for other arthropods and top predators, such as birds. Lycosidae, i.e. *Arctosa cinerea, Arctosa perita, Pardosa agricola*, were chosen to be the object of this study because they serve as good representatives for specific habitats of beaches (Vahder and Irmler 2010). In this paper, we address the following questions: 1) How large is the population size of the three species of Lycosidae on two closed beaches? 2) What is the distribution and home range of Lycosidae at beaches in general? 3) Do the observable movement patterns of *A. cinerea* differ between a non-accessible nature conservation beach and an accessible beach? 4) What conclusions may be drawn for beach management that is adapted to the requirements of predatory terrestrial arthropods?

4.2. Material and method

4.2.1. Studied species

Arctosa cinerea (Fabricius, 1777), *Arctosa perita* (Latreille, 1799) and *Pardosa agricola* (Thorell, 1856) are Lycosidae that inhabit coastal areas. *Arctosa cinerea* is a typical species found in sandy beaches with a low proportion of shingle (Vahder and Irmler 2010). It also inhabits gravel pits (Sacher 1992) and riverbanks, for example, in the Alpine region (Framenau et al. 1996). At the Baltic Sea coast, *P. agricola* mainly inhabits shingle and gravel beaches (Knülle 1951; Vahder and Irmler 2010). Both spider species prefer sparsely and non-vegetated grounds and may also be observed along rivers at areas where these conditions are found. *Arctosa perita* prefers sandy semi-fixed foredunes

(Schultz and Finch 1990) but also uses sandy beaches (Bell et al. 1998; Vahder and Irmler 2010). Lycosidae are known to be generalist predators; they mainly feed on insects and other spiders (Foelix 1979; Nyffeler and Benz 1988). All observed Lycosidae were terrestrial spiders with brood caring females (Palmgreen 1944, Foelix 1979) with a biennial life cycle (Schaefer 1976). *Arctosa cinerea* was observed to move landward towards burrows in the ground in order to survive unfavourable conditions in the autumn (Framenau et al. 1996). *Arctosa perita* is able to dig burrows into the ground to a depth of 30 cm, preparing the walls with a net of fine silk to survive winter (Kirchner 1987). Species were identified using Heimer and Nentwig (1991); nomenclature of species followed Platnick (1993).

4.2.2 Study sites

The investigations performed on Lycosidae were conducted at three Baltic Sea beaches. The two beaches Stakendorf (STA) and Schleimuende (SCH; Table 4.1) are part of nature conservation areas. In STA, tourists were allowed to access the lower beach area, whereas the backshore and foredunes were closed off. In SCH, the entire beach area was closed to tourists. Beach cleaning measures were not conducted on any beach. For the observation study, we used an accessible beach area (AB) used as a tourist site and located close to STA. Beach AB is regularly cleared of sea debris and the sand is replenished in spring.

Table 4.1: Site conditions at the two nature conservation beaches.

Beach site		Schleimuende	Stakendorf
Abbreviation		SCH	STA
Coordinates		N 54° 41.702873	N 54° 24.130980
		E 10° 01.548402	E 10° 26.748460
Conservation		closed	closed upper beach area
Beach width		10-17 m	20-28 m
Soil texture	Stones	3.2 ±0.6 %	12.2 ±2.8 %
	Gravel	10.3 ±2.6 %	11.9 ±2.9 %
	Sand	73.0 ±3.1 %	60.0 ±4.0 %

4.2.3 Mark-recapture experiment

4.2.3.1 Study design

On the closed Baltic Sea beaches, Stakendorf (STA) and Schleimuende (SCH) at the upper shore, 120 individually marked pitfall traps with a diameter of 100 mm were installed in three rows. The row with the greatest distance to the shore was placed at the foot of the beach ridge. The other two rows were placed in 3 m apart from each other running towards the waterline. The whole observed upper shore area was about 720 m² extent at both beaches. In order to investigate the population size and movement behaviour, the mark-recapture method was applied for the three species *A. cinerea, A. perita* and *P. agricola* from March 2012 to September 2012 at Stakendorf (STA) and from April 2013 to September 2013 at Schleimuende (SCH). During the experiment, traps were

kept open and were checked and emptied three days a week. Specimens were marked individually with a bee tag glued to their cephalothorax using a cyane-acrylate based adhesive (Framenau 2005). Specimens that were smaller than 10 mm were marked on the legs according to a predetermined code (Framenau et al. 1996). Sex and body length (1 mm accuracy) were determined for each specimen. To minimise the influence on spider population development, individuals carrying spiderlings or egg sacs were not examined.

4.2.3.2 Data analysis

Data analyses were calculated using the statistical program R 3.1.2 (R Development Core Team 2014, Vienna, Austria) if not otherwise specified. The data analysis of spider distribution using the number of catches in the traps began with a log-transformation to achieve normally distributed data. The appropriate statistical linear mixed effect model included the distance of row of trap to the shore (row) as a fixed factor. To focus on general trends rather than specific trait patterns in the distribution along the shore, beach and species were included as random effects into the model to include the nested design (Bonte and Maes 2008; Zuur et al. 2009). Based on this model, an ANOVA was applied.

For the estimation of the home range of individuals of Lycosidae that were recaptured at least five times, the minimum area method was used (Odum and Kuenzler 1955, Samietz and Berger 1997). Home range data were entered into ArcMap 10 (ESRI, Redlands, CA) to calculate the degree of overlap of minimal complex polygons for *A. cinerea*. Also, the largest home range span was calculated as the maximal distance within the polygon. Appropriate linear mixed effect models were defined to assess the responses of the home range parameters "minimal complex polygon" and "home range span" to the number of catches of *A. cinerea* (N = 130; Verbeke and Molenberghs 2000). Based on a graphical residual analysis, the data were normally distributed and heteroscedastic due to different number of catches and to different beach sites (beach). The statistical model included total number of recatches of each specimen (catch) as a fixed covariable and the variables sex of specimen (sex), beach site (beach) as well as their interaction (beach x sex) as fixed factors. To consider the variety of specimens, body size (body) was regarded as a random factor (Zuur et al. 2009). Based on this model, an ANCOVA was fitted. After this, multiple contrast tests (Bretz et al. 2011) compared the several levels of the influencing factors. Home range data of *A. perita* (N = 6) and *P. agricola* (N = 1) were not statistically analysed, because of low sample size.

Data analysis of the body size started with the definition of an appropriate statistical linear mixed model for each species separately (Verbeke and Molenberghs 2000). The data were normally distributed, based on a graphical residual analysis. The statistical models included beach site (beach), sex of specimen (sex) and their interaction (beach x sex) as fixed factors. Based on this model, an ANOVA was conducted. After this, multiple contrast tests (Bretz et al. 2011) compared the several levels of influencing factors.

The population sizes of the three species were estimated separately for each beach using the program MARK (Version 6.1, White and Burnham 1999) with a Cormack-Jolly-Seber model (Seber 1986). Models were tested with a goodness of fit test using the integrated program RELEASE in MARK. Population size was estimated using the POPAN model formulation (Schwarz and Arnason 1996) that postulates the existence of a super-population from which animals may enter the surveyed population. The model formulation consists of three parameters: ρ_i as encounter probability at occasion i, ϕ_i as probability of survival between sampling occasions i and i+1 and b_i, which is the probability of an animal entering from the postulated super population (White and

Burnham 1999; Cooch and White 2013). Where necessary, encounter occasions were pooled to allow estimation or to reduce confidence intervals. Separate models with differences in time dependence and encounter probability were tested using Akaike's Information Criterion (Burnham and Anderson 2002). Finally, models with a constant encounter probability but time-dependent survival and entrance probability were chosen as best fitting models.

4.2.4 Observation of spider movement

4.2.4.1 Study design

Movement patterns of *A. cinerea* were observed directly at the closed nature conservation area STA and the tourist-accessible beach near the conservation area (AB) during summer 2013. Twenty-five spiders were caught at STA and were carefully marked with a bee-tag glued to their cephalothorax for easier visibility. Thirteen specimens were released at AB and 12 at STA. After allowing time for acclimatization, the observer marked each change of direction in movement of each spider for one hour. A distance of at least three meters between observer and spider and slow movements of the observer were maintained in order to minimise disturbance. Distance between marked spots and the time of movement was recorded. In addition, the distance between the outermost points and distance to the shoreline at the beginning and the end of each observation were measured. Furthermore, body length (1 mm accuracy) of spiders was measured and the temperature of the soil was recorded at the beginning and end of the observation period. Some 102 tourists passed through the accessible beach (AB) during the observation of spiders.

4.2.4.2 Data analysis

Data analysis of the speed, length and duration of movement as well as the duration of rest for each step of the observation began with the definition of a statistical linear mixed effect model. Homogeneity of data was achieved by taking the logarithm of data as proven by graphical residual analysis. The statistical model included the covariable soil temperature (soil) and the variable beach access (access) as fixed factors. To include the nested design, specimen (ID) was taken as a random nesting factor (Zuur et al. 2009). Additionally, the total length of movement and the directness of movement of each spider were analysed with appropriate statistical linear mixed models. Directness of movement was defined as radius from first to last step divided by total length of movement. The statistical model included the covariable soil temperature (soil) and the variable beach access (access) as fixed factors. An ANCOVA was conducted to test whether fixed variables and covariables influence the response variable significantly, for all models.

Direction of spider movement was assigned as either landward or as seaward according to the difference of distance to the shore at the beginning and the end of observation. Thus, binomial data analysis started with the definition of a logistic regression using a generalized linear mixed model with the logit-link function. Beach access (access) was included as a fixed factor that significantly influenced the result of the model. An ANOVA using χ^2 was applied to answer the question of the trial.

4.3. Results

4.3.1 General distribution of spiders and home range estimations at the shore

The distribution of spiders differed with distance to the shore (Figure 4.1). Indicated by the number of catches per trap, traps placed in the row at the lower shore were significantly less frequented by spiders ($p < 0.05$).

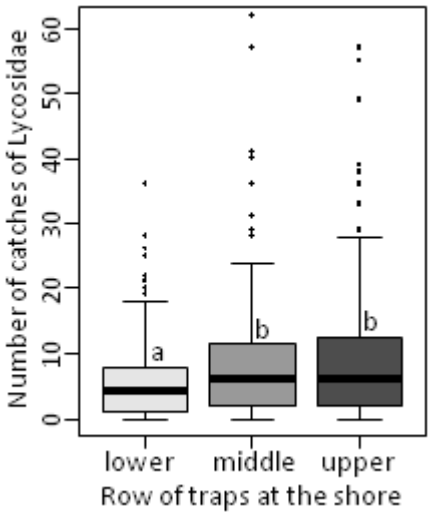

Figure 4.1: General spider distribution within three different distances to the shore as absolute number of catches in the traps. Different lower case letters indicate significant differences ($p < 0.05$) derived by multiple contrast tests based on a linear mixed effect model (row as fixed effect: num/den DF: 2/712; F: 27.47; $p < 0.001$).

The minimal complex polygon and home range span of *A. cinerea* were significantly correlated to the number of catches (Figure 4.2; Table 4.2). The size of the minimal complex polygon was not influenced by spider sex, but was affected by beach (Table 4.2). Mean size of the minimal complex polygon for males of *A. cinerea* was 143.18 ±2.62 m² (164.70 ±13.48 m² females) in SCH and was significantly larger in STA with 182.60 ±3.46 m² for males (179.36 ±47.89 m² females; Figure 4.2). The largest minimal complex polygon of all observed spiders was 445.5 m². Spider males had a mean home range span of 75.57 ±2.92 m, whereas the female's span was smaller with 58.16 ±9.01 m (Figure 4.2). However, this difference was not significant (Table 4.2). Home range overlap was highest for males of *A. cinerea*. In SCH, 13.7 % (STA: 7.7 %) of the area of multiple complex polygons of males did not overlap at all, while with females in SCH 73.4 % (STA: 28.8 %) of them did not overlap. Beaches also differed according to the degree of overlap. Male spiders at STA had more than five overlaps in their area of minimal complex polygons in 71.3 %, while at SCH it was only 39.2 %.

The maximal size of a minimal complex polygon of *A. perita* was 173.70 ±43.15 m²; the largest home range span was 78.66 ±13.36 m in the polygon. For *P. agricola*, the only individual with more than five catches had a minimal complex polygon of 166.50 m² and a home range span of 111.00 m.

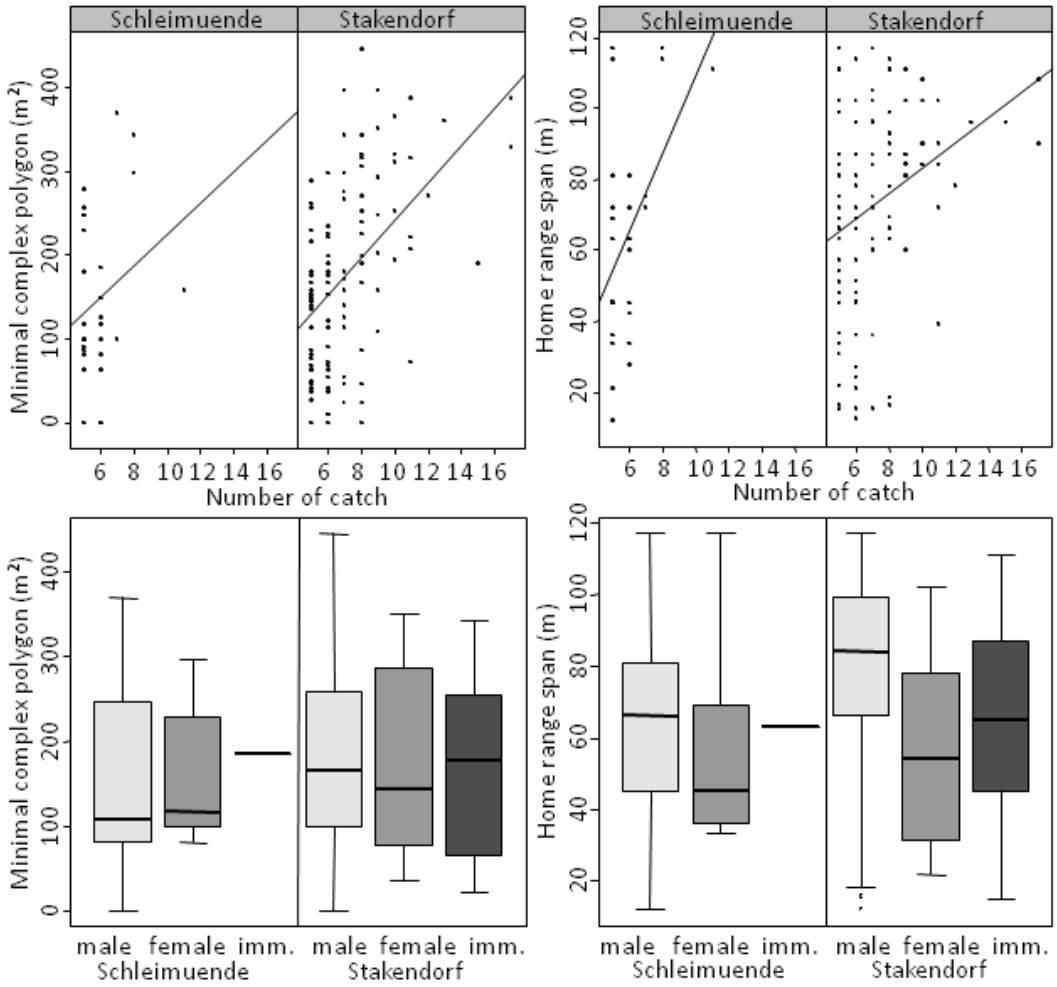

Figure 4.2: Home range of *A. cinerea* (at least 5 catches per specimen; N=130) calculated as minimal complex polygon (Odum and Kuenzler 1955) and home range span.

Table 4.2: The effects of the covariable total number of recatches of each specimen (no. of catch), the fixed variables sex of spiders (sex), beach type (beach) and their interaction (beach x sex) on the minimal complex polygon and home range span of *A. cinerea*. F-values and p-values were derived from appropriate statistical models.

Response	Fixed effects	num / den DF	F	p
Minimal complex polygon (m²)	no. of catch	1 / 118	130.86	<0.001
	sex	1 / 118	2.35	0.10
	beach	1 / 118	4.89	0.03
	beach x sex	1 / 118	2.41	0.12
Home range span (m)	no. of catch	1 / 118	47.18	<0.001
	sex	1 / 118	0.77	0.38
	beach	1 / 118	0.24	0.63
	beach x sex	1 / 118	0.00	0.95

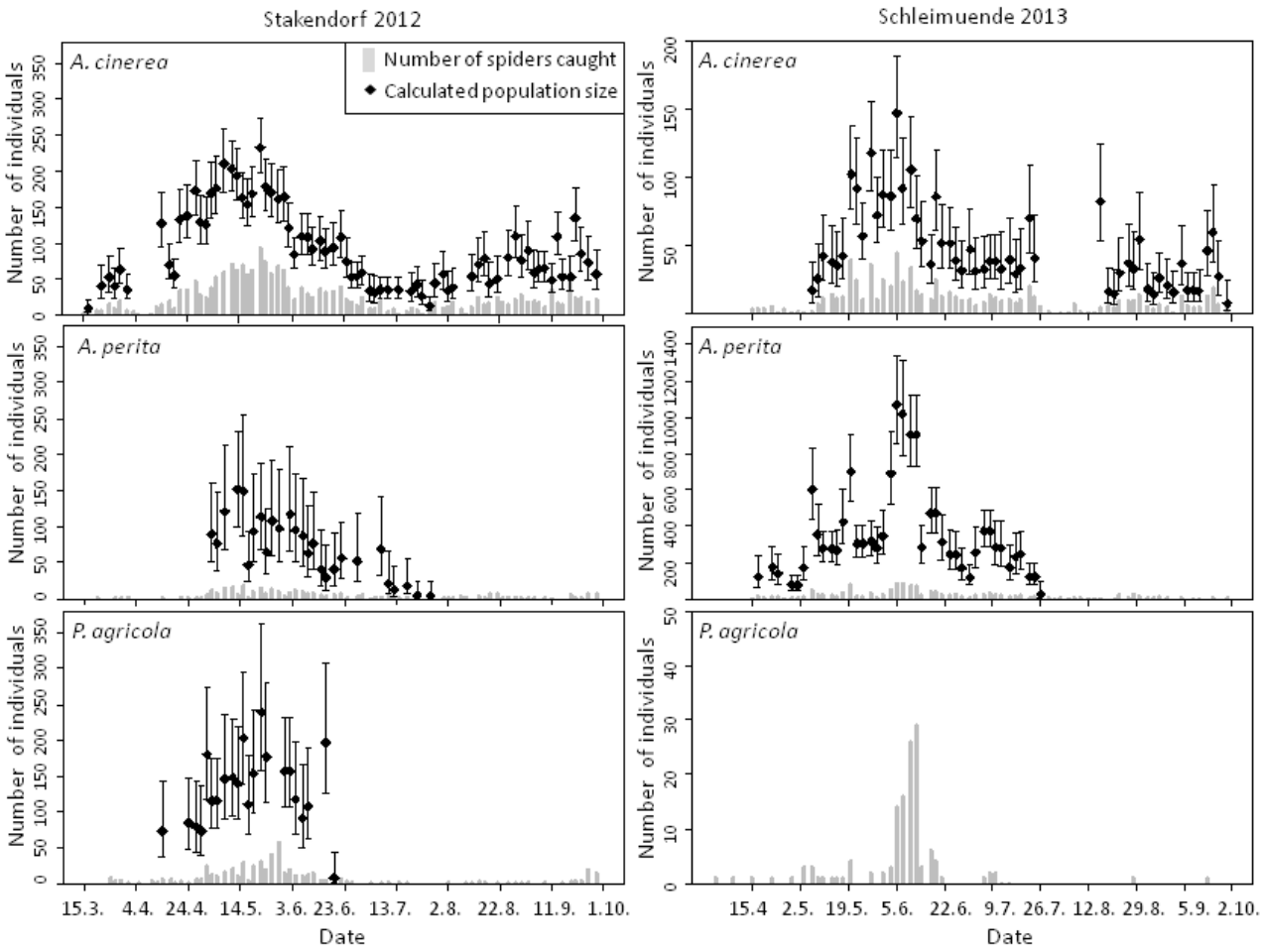

Figure 4.3: Number of species caught and estimated population sizes using the POPAN model (Schwarz and Arnason 1996) for the species *A. cinerea, A. perita* and *P. agricola* at Stakendorf in 2012, and Schleimuende in 2013.

4.3.2 Population dynamics

In total, 982 specimens of *A. cinerea*, 193 specimens of *A. perita* and 366 specimens of *P. agricola* were caught during the mark-recapture experiment at the beach of Stakendorf (STA) in 2012. In 2013, at the beach of Schleimuende (SCH), 425 specimens of *A. cinerea*, 937 specimens of *A. perita* and 116 specimens of *P. agricola* were trapped. Body size varied between species and sex. Females had significantly larger body size than males for all species. Additionally, any species of spiders at STA were significantly larger than in SCH, e.g. females of *A. cinerea* in STA 13.0 ±0.1 mm, in SCH 11.6 ±0.2 mm ($p < 0.01$), males *A. cinerea* 12.4 ±0.1 m in STA and 10.6 ±0.1 m in SCH ($p < 0.001$), males of *A. perita* 6.9 ±0.1 mm in STA and 6.7 ±0.1 mm in SCH ($p < 0.001$), females of *A. perita* 7.8 ±0.1 mm in STA and 7.2 ±0.1 mm in SCH ($p < 0.001$), males of P. agricola 6.2 ±0.1 mm in STA and 6.1 0.1 mm, in SCH ($p < 0.001$), and females of P. agricola 7.3 ±0.1 mm in STA and 6.5 ±0.3 mm in SCH ($p < 0.001$).

Using the model POPAN (Schwarz and Arnason 1996), the estimated population size resulted in a mean of 90.6 ±53.9 individuals for *A. cinerea* in STA (Figure 4.3). A peak of 232.7 ±18.6 individuals was caught at the end of May. In SCH, the population size of *A. cinerea* was 47.21 ±29.8, with the largest population size 146.6 ±18.6 at the beginning of June (Figure 4.3). The estimated population size of *A. perita* was 70.5 ±41.8 in STA and 348.3 ±254.2 in SCH (Figure 4.3). The maximal population

size of *A. perita* was 152.2 ±32.8 at mid-May in STA. In STA, the mean population size of *P. agricola* was 131.1 ±52.5 (Figure 4.3), and the maximum size was 239.5 ±51.5 individuals. Individuals of *P. agricola* that were re-caught in SCH were too low for a substantial population analysis. Nevertheless, a maximum of 29 specimens was caught at mid-June (Figure 4.3).

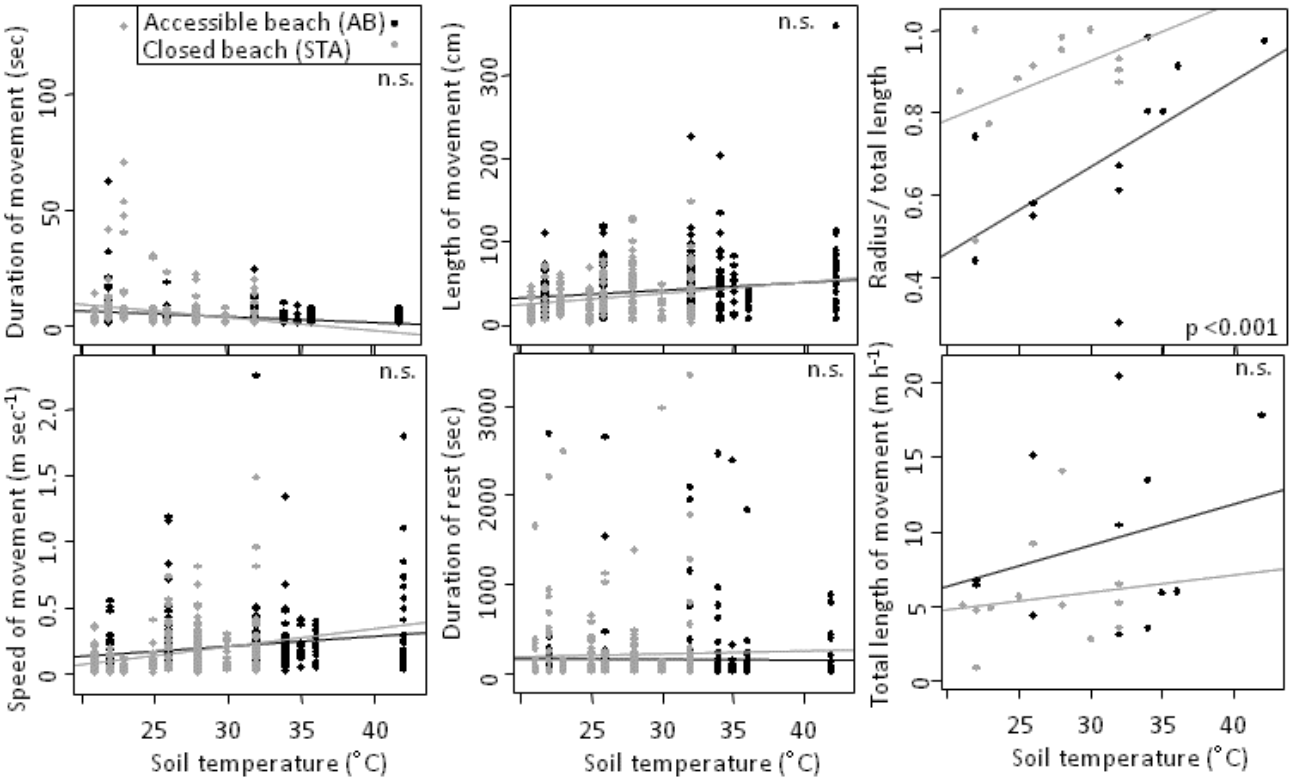

Figure 4.4: Correlations of observed movement of *A. cinerea* with soil temperature in regard to duration, speed and length of movement as well as duration of rest. In addition, total length of movement and directness of movement (radius vs. total length of movement) are given. Significant differences between beach accessibility are indicated in the graph. Statistics were derived from linear mixed effect models for which parameter estimates (p-values) are given in Table 4.3.

4.3.3 Movement patterns

Due to the large variation in movement behaviour between specimens, observed movement patterns per step duration, speed and length of movement as well as duration of rest did not differ between different levels of beach accessibility (Figure 4.4; Table 4.3). Duration and speed of movement were influenced by soil temperature. Speed of movement increased with increasing soil temperature, whereas duration of movement decreased. Duration of rest was not influenced by soil temperature, which stayed rather stable at a mean rest level of 177.2 ±19.8 sec (Figure 4.4; Table 4.3).

The total length of movement of *A. cinerea* was smaller at the conservation area (5.61 ±0.96 m h^{-1}) than at the accessible beach (9.42 ±1.70 m h^{-1}). However, this differences was not significant ($p = 0.19$). Furthermore, the degree of directness of movement, which was calculated as distance between the outermost points and total length of movement, was significantly higher at the conservation area (0.88 ±0.04) than at the accessible beach (0.70 ±0.06; $p < 0.001$, Table 4.3). Direction of movement was more focused towards the sea at the accessible beach (seaward: 8 specimens;

landward: 4 specimens) than at the conservation area (seaward: 2 specimens; landward: 10 specimens).

Table 4.3: The effects of the covariable soil temperature (soil) and the fixed variable beach accessibility (access) are given for the data of direct observation of *A. cinerea* movement. For speed, duration and length of movement and duration of rest, the F- and p- values were derived from appropriate statistical linear mixed (effect) models. Additionally, the effects of soil temperature (soil) and beach accessibility (access) on the direction of movement are given. χ^2-values were derived from an appropriate generalized linear model using the binomial function.

Response	Fixed effects	num / den DF	F	p
Duration of movement (sec)	soil	1 / 439	3.90	0.049
	access	1 / 22	0.13	0.73
Speed of movement (m sec^{-1})	soil	1 / 439	6.88	0.01
	access	1 / 22	0.46	0.51
Length of movement	soil	1 / 439	1.37	0.24
per step (m)	access	1 / 22	0.26	0.61
Duration of rest (sec)	soil	1 / 439	0.35	0.55
	access	1 / 22	1.51	0.23
Directness of total movement	soil	1 / 22	2.44	0.13
(Radius/total length)	access	1 / 22	14.80	0.001
Total length of movement (m h^{-1})	soil	1 / 22	3.35	0.08
	access	1 / 22	1.80	0.19

Response	Fixed effects	num / den DF	(LR) χ^2	p
Direction of movement	soil	1 / 22	0.54	0.10
	access	1 / 22	4.41	0.04

4.4. Discussion

4.4.1 Home range, mobility and population size

In contrast to *A. cinerea* at riverbanks in the Alpine region (males: 210 m², females 130 m²; Framenau et al. 1996), the observed minimal complex polygon of *A. cinerea* at the Baltic Sea was considerably smaller. Discrepancies were based on the varying study designs as well as differences in habitat structure. Gravel beds formed wide bars and islands along rivers (300 to 500 m width; Framenau et al. 1996) whereas the observed beaches were linear habitats with a maximal width of 17 to 28 m. The correlation of the minimal complex polygon and number of catches indicated that the study design influenced the outcome. Nevertheless, the minimal complex polygons generally underestimated the real home range area (Samietz and Berger 1997). The greater overlap in the home range of male wolf spiders than of female wolf spiders was a typical behaviour for non-terrestrial spiders; the females were more immobile due to brood care (Kuenzler 1958).

Localisation of overlap areas indicated that males were inclined to greater activity and would travel alongshore to search for suitable mating partners (Framenau et al. 1996), which also suggested greater male-male competition (Framenau 2005).
The upper shore area was identified to be a main critical area for disturbance derived by the number of catches per trap. A higher abundance of spiders on the upper shore, despite zonation (Irmler et al. 2002; Bonte and Maes 2008; Vahder and Irmler 2010), was explained by the escape from periods of inundation (Framenau et al. 1996; Lambeets et al. 2010). Additionally, *A. cinerea, Trochosa ruricola* and *Venatrix lapidosa*, all Lycosidae inhabiting shores of river banks, were observed to move landward during periods of brood care (Hackmann 1957; Framenau et al. 1996; Framenau 2005).
Differences in population size as well as body size of spiders between beaches might be due to different years and different abiotic conditions of the sites. Stones in Stakendorf provided easy hiding and shading areas, whereas the beach of Schleimuende had few stones, which forced spiders to expend energy-demanding burrowing behaviour or travelling (Knülle 1951; Framenau et al. 1996). Soil structure also explained the greater occurrence of *A. perita*, which prefer sandy dunes (Vahder and Irmler 2010) at Schleimuende. *Pardosa agricola*, which prefer stony and gravel beaches (Vahder and Irmler 2010), had a greater number of catches at Stakendorf which had a higher proportion of shingle. Furthermore, the arthropod composition at the beaches varied. Diptera as prey species and Pompilidae as predators were mainly found in Stakendorf, whereas mainly Gammaridae as possible prey species and several specimens of *Broscus cephalotes* as predators (Schierding et al. 2013) were found at the beach of Schleimuende. Many studies give only species density rather than population size (e.g. Framenau et al. 1996), which is a consequence of the need for reliable numbers of re-caught specimens. Since only spiders larger than 5 mm were marked and brood-caring females were neglected, population estimates of this study might be too low. Furthermore, loss of tags by moulting led to an underestimation of survival probability and overestimation of probability of entrance (Kuenzler 1958). Population dynamics of *A. cinerea* at the Baltic Sea with a peak and females carrying egg sacs in May and just a few specimens at the end of July were in accordance with observations of Schaefer (1976). But this differs from population dynamics in the Alpine region, where females carrying egg sacs occurs later, in June and July/August (Framenau et al. 1996).

4.4.2 Impact of tourism on spider movement patterns

The hypothesis that *A. cinerea* would change speed or length of movement due to disturbance was not supported by observation data. The high correlation to soil temperature indicates that environmental and physiological conditions were more important than disturbances (Beale and Monaghan 2004). Frequency and duration of rest was also controlled by the need to restore physiological functions such as thermoregulation (Kuenzler 1958; Humphreys 1987) and muscle exhaustion (Foelix 1979). Nevertheless, with disturbance, *A. cinerea* directed its movement towards the shoreline. *Arctosa cinerea* is generally aware of the direction of the shore, and usually directs its movements inland to escape at events of inundation (Papi and Tongiorgi 1963) it also reacts with a startle response towards wet sands (Knülle 1951). We propose that, despite the possible danger of waves at the shore, *A. cinerea* escapes along the shore from disturbances using the wet line as orientation. In addition to the influence on spider behaviour, habitat conditions were unfavourable at the accessible beach where burrows are exposed to a higher probability of destruction and where fewer prey species are available (Nyffeler and Benz 1988; Schierding et al. 2011). Furthermore, drift

line material was missing due to beach cleaning measures for tourism. Drift line material provides a substantial food source for possible prey species (Knülle 1951; Llewellyn and Shackley 1996, Weslawski 2000) and supports moderate conditions under the drift in comparison to the open xeric sand (Barnes and Barnes 1954). Barnes and Barnes (1954) observed a high occupancy of especially immature specimens of *Arctosa littoralis* to drift line material.

4.4.3 Management application

This study underlines the need to improve nature conservation for terrestrial arthropods at beaches. First of all, the upper shore was identified as the main critical habitat area for disturbance of Lycosidae at the beach. Trampling by beach visitors destroys vegetation, changes arthropod communities, damages burrows of spiders and affects spider movement (Liddle 1975; Weslawski 2000; Bonte and Maes 2008; Schierding et al. 2011). Nevertheless, beach access is important for tourism at the coast and is a prime factor in beach vacation destinations (Haller et al. 2011). Thus, beaches closed for reasons of nature conservation interfere with economic interests and, therefore, are areas of great conflict for stakeholders (Haller et al. 2011). Beaches with an accessible lower shore and seawater area, but closed-off upper area (a minimum of one-third) would be a compromise between nature conservation and beach tourism. This management excludes the most critical areas from access because trampling has less impact on beach ecosystems than trampling in upper beach areas (Brown and McLachlan 1990). Beaches are linear habitats, which allow species to travel along the shore in two directions only. Barriers for spiders, such as intensively accessed tourist beaches, harbours or constructions for coastal defence, may easily isolate arthropod populations at the beach. Loss of connectivity would increase the effects of disturbance and disrupt re-population of abandoned sites as well as the flow between sub-populations (Gilpin 1987; Bonte and Maes 2008; Lambeets et al. 2010). Furthermore, the size of sub-populations should at least match the minimum viable population size. Due to the high risk of isolation and the great frequency of natural disturbance, the minimum viable population size may need to be set at a value higher than in more connected and less perturbated systems (Goodmann 1987). According to the population density and home range of *A. cinerea*, we estimate the length of the minimal conservation area to be at least 1.5 km (Mühlenberg et al. 1991). To enhance connectivity between sub-populations and create relatively undisturbed habitats, closing the upper beach area parallel to the shore is urgently needed in beach conservation strategies. Tourists generally prefer sandy beaches. Therefore, conservation areas are often placed on beaches with a greater stone content and exposition to the sea to reduce conflicts with tourist interests. Nevertheless, investigated species showed differences in habitat abundance (Schultz and Finch 1990; Vahder and Irmler 2010), which underlines the necessity of variability in soil components and exposition of beach conservation areas. Arthropod populations of beaches face the problem of an increased inundation during winter or, in future scenarios, inundation by sea level rise. Due to the need to retreat upward or even into the hinterland during inundation events (Knülle 1951; Framenau et al. 1996), an appropriate and conserved hinterland is necessary. Species of coastal areas chose the harsh conditions partly to reduce competition with grassland species (Bethge 1973; Irmler et al. 2002). Beach use by tourism increases the competition among species that are usually separated by preference for different habitats, leading to cumulative effects of beach access on arthropod populations.

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Picture G: ***Arctosa cinerea*** **at the beach at Schleimuende.**

Picture H: ***Arctosa perita*** **at the beach at Schleimuende.**

Chapter 5

Tourism and near natural beaches at the Baltic Sea – a contradiction?

The present study was initiated to develop a framework for sustainable beach management at the Baltic Sea, including the requirements of fauna and flora as well as needs of stakeholders, especially tourists. The beach can provide several ecological and social functions that require different and contradicting ideal prerequisites (Table 5.1). The contemplation of different management ideas in regard to their impact on ecosystem functioning and services of beaches is necessary for achieving success.

The beach provides habitats for reproduction, migration and food resources for terrestrial fauna (e.g. Lycosidae, Carabidae and Avifauna; Schultz and Finch 1990; Vahder and Irmler 2010; Schierding et al. 2011) and marine species (e.g. Crustacea; Brown and McLachlan 1990; Jędrzejczak 2002). It also serves as seedling, establishing, growing and reproducing area for terrestrial flora (Berg et al. 2004). Plants at the beach function as primary stabilizers of sediments at shores (Berg et al. 2004), creating a barrier. This first barrier provides sheltered conditions for less robust plant species and more moderate habitat conditions for several faunal species. The initiation of the dune chronosequence begins with the establishment of plants at the beach (Berg et al. 2004; Martinez and Psuty 2004; Labuz and Grunewald 2007; Ellenberg and Leuschner 2012). The beach is a buffer zone against erosion of dunes and the hinterland, which can partly be controlled by beach vegetation (Martinez and Psuty 2004; Barbier et al. 2011). Thus, the beach supports the development of a natural coastal defence of ecosystems in the hinterland and helps regulating the impact of the sea on the hinterland.

Regarding economic interests, beaches have great value for tourism. The beach is the main destination for tourist recreation at the Baltic coast (Barbier et al. 2011; Haller et al. 2011). This is, of course, based on great recreational value and the direct vicinity to the water. Furthermore, water related sports activities like surfing or fishing are directly connected to the beach (Hall 2001). When selecting a beach, tourists choices are mainly correlated to sandy sediment, beach width and clean water conditions (Hallermeier 2011). In addition, facilities such as toilets, shops and parking lots are taken into account (Jędrzejczak 2004). Tourists expect clean beaches without drift line material, forcing municipalities to take actions (Dolch 2002; Jędrzejczak 2004; Kessler 2008; Mossbauer et al. 2012).

All these tourism promoting actions interact with the ecosystem functions regarding habitat for fauna and flora at the beach. The beach was identified to be a highly vulnerable ecosystem in regard to trampling, which leads to vegetation loss, sediment erosion and abrasion (Brown and McLachlan 1990; Andersen 1995; Brown and McLachlan 2002; Lemauviel and Rozé 2003; Seer et al. submitted 2015). Destruction of beaches by human use also accelerates cumulative effects on the hinterland and the entire coastline (Hall 2001). Within the last few years, we worked on identifying the conflict in detail. We carried out several experiments and studies on beach fauna and flora as well as observations of beach visitors' behaviour, stakeholder interviews and discussions on workshops. The research aimed to find measures that take the improvement of ecological conditions at the beach and requirements of beach visitors into account. Analysis of

Table 5.1: Main ecosystem functions and main prerequisites for the provision of functioning for sandy beaches.

Ecosystem functions		Prerequisite
Habitat	Provision of suitable environment for fauna and flora. Provision of food/nutrients, water, hiding areas and possibilities of reproduction, etc.	Undisturbed beaches
Development	Development of new ecosystems with further functioning (e.g. dunes, near shore lakes)	Undisturbed beaches with possibilities of establishment and existence of plants at the beach.
Regulation	Regulating and buffering impacts of the sea on the hinterland by reducing salt content, reducing energy input, controlling erosion, etc.	Establishment and continuity of plants for erosion control and development of beach ridges
Coastal defence	Sheltering the hinterland from flooding events	Establishment and continuity of plants for erosion control and development of beach ridges
Research and education	Providing information and knowledge on geomorphology, hydrology, flora and fauna, etc.	Beach access
Tourism	Providing areas with high value for human welfare and recreation. Leading to economic interests	Beach access for tourists. Fine sands, clean beaches, infrastructure and facilities

differently-used beaches clearly identified botanical and functional differences between closed and open beaches (Seer et al. submitted 2015; Chapter 2). Via experiments, these results could be linked to the trampling-sensitivity of beach plants (Seer et al. accepted 2015; Chapter 3). Currently, coastal conservation areas in Germany primarily focus on the exclusion of tourists for the safety of breeding and migrating birds, while flora and remaining fauna are rarely addressed. Signs and small fences protect the beach ridge in many areas as an important zone for coastal defence. Analysis of habitat requirements of Lycosidae and observation of *Arctosa cinerea* at the beach helped to create guidelines for a beach conservation management plan that also addresses space demands of beach organisms (Seer et al. 2015b; Chapter 4).

Stakeholder interviews with members of regional and superregional parties at three different municipalities in Schleswig-Holstein (Lindhöft, Surendorf, Hohenfelde) revealed heterogeneous attitudes towards the beach (Seer et al. 2015a). Most of the interviewees (75 %) were concerned about the future of the beach and recognized the sustainable management and the protection of

beaches as a central future task. However, the loss of amenity value for tourism due to nature conservation measures, which would also lead to financial losses, was the greatest fear of all professions. The total separation of nature conservation and tourist beaches was always questioned. Nevertheless, a partial or temporal exclusion of beach accessibility with free access to the water might be tolerable for beach visitors. Furthermore, the interviews revealed that local stakeholders have a strong personal attachment towards "their beach" which could easily raise emotionally-driven prejudices against any measures. Therefore, most stakeholders nominated "soft actions" such as education and sensitization of beach visitors as primary measure (Seer et al. 2015a). A successful implementation of nature conservation tasks could just be fulfilled, with a great personal interest of local stakeholders. They should participate in a process oriented development of a superregional management of beaches.

Based on the results of this project and literature reviews, several management concepts affecting beach ecology directly are taken into consideration. Of course, all addressed management concepts try to respect nature conservation as well as tourism:

a) Entirely closed-off beaches

The total exclusion of beach visitors at nature conservation areas or national parks is currently the key measure of management for beach preservation (Santoro et al. 2012; Fenu et al. 2013). By closing the entire shore, the total sea-to-land gradient is preserved and maintenance of species and beach functions is assured, under the prerequisite that the closed area is large enough. In a beach area in Italy, flora quickly regenerated after closing off the beach, showing that a high regeneration potential of this ecosystem still exists there (Santoro et al. 2012; Acosta et al. 2013). The high regeneration potential of beach flora could be related to the preadaptation of beach vegetation to harsh abiotic conditions such as salt spray or burial and to the regular input of seeds by the ocean (Andersen 1995; Garcia-Mora et al. 1999; Lemauviel and Rozé 2003; Santoro et al. 2012). Furthermore, in contrast to other ecosystems (Kissling et al. 2009), regular impacts of the sea might prevent long term trampling effects on the soil (e.g. changes in pH, soil compaction, soil organic matter content) and thus allowing easier regeneration.

However, local stakeholders and beach visitors might not accept a total exclusion of access to the beach. Interviews with stakeholders showed that beach access and the possibility to enter the water are the main prerequisites for any conservation measure (Haller et al. 2011; Seer et al. 2015a). On one hand, this can be explained by the high economic value of beach tourism. On the other hand, local stakeholders have a strong personal attachment to the beach (Seer et al. 2015a). Local stakeholders think of their beach as their own property. This strong attachment is often underestimated and must be taken into account to prevent an escalation of conflict.

b) Partial exclusion of beach visitors

In several nature conservation areas, a fence running parallel to the waterside not only closes off the beach ridge, but also the upper shore, which is usually the upper third or half of the beach. In this way, the most sensitive area for plants of the Cakiletea maritimae and the Honckenyo-Elymetea is excluded from beach access. Also, the upper beach area was identified to be the most frequented habitat of wolf spiders in this study (Seer et al. 2015b). Brown and

McLachlan (1990) already proposed this zone to be the most sensitive area to disturbances, because of the fragile initiation of dune development at the beach. Thus, the main ecological functions e.g. regulation and habitat may be maintained by closing off the upper shore and the beach ridge. Unfortunately, vegetation relevés at beaches indicated that plant communities at partially closed off beaches showed differences in plant trait patterns in contrast to fully closed off beaches (Seer et al. submitted 2015). Nevertheless, stakeholders at less intensively-used beaches might accept partial exclusion more easily than total exclusion because beach access and the passage of beaches along the shore are guaranteed.

In general, this type of beach management needs shores that are wide enough to allow a sufficient coexistence of visitors and beach organisms. Fences at the shore must be removed in autumn and reinstalled in spring; otherwise, winter floods and storms would demolish them. Therefore, the trampling impact on the upper shore can only be avoided during summer season and this practice is costly and labour extensive.

This concept is already practiced at three nature conservation areas of Schleswig-Holstein (Strandseenlandschaft Schmoel, Kleiner Binnensee bei Behrensdorf and Wasservogelreservat Wallnau). The fences in Kleiner Binnensee bei Behrensdorf are generally accepted and are often even positively used by beach visitors (e.g. to dry towels). In contrast, the great number of beach visitors in Strandseenlandschaft Schmoel might hinder the successful breeding of sand plovers (*Charadrius hiaticula*) and questions the applicability of the measure.

c) Beach enlargement

Defeo et al. (2009) proposed the coastal squeeze as the main threat for sandy beaches worldwide. Rising sea level and increasing shoreline erosion due to climate change, increase of coastal defence measures and increase in human population will shorten beach width. A wider beach with higher sand disposal by waves and currents might reduce pressure from beach visitors on beach organisms. As it is, concepts like partial beach closing parallel to the shore need beaches that are large enough to allow a coexistence of beach organisms and beach visitors. This makes beach enlargement a major issue in sustainable beach management. This could, for example, be achieved by the creation of substantial setbacks that allow the coastline to shift inland (Defeo et al. 2009).

Furthermore, ways to increase or sustain sediment accumulation at the beach should be found (Brown and McLachlan 2002). In the Netherlands, the Zandmotor, a 128 hectar large new sand area, was created from 21.5 million m³ sand (ARTIFICAL ISLAND Location Ter Heijde, Zuid-Holland, Netherlands). The natural transportation of sediment along the shore should create 35 hectares of new beaches that should help to defend the coast against sea level rise in context with climate change, to sustain the beaches for tourism and to supply the dunes with new sand material. The project also includes an area specified for flora and fauna on the new peninsula. The "sand motor" shows a synergy of coastal defence, tourism and nature conservation. Still, the development potential of this high impact level measure needs further research and observation of sediment processes and biotic impacts. This concept is not feasible at the Baltic Sea in Schleswig-Holstein because the Schleswig-Holstein bight does not consist of enough sandy sediment and primarily contains hard bottom substrates (Bohling 2009; Niedermeyer et al. 2011). Here the sediments that are transported along the shore usually originate from cliffs

or seashore abrasion (Schwarzer 2010). Thus, omitting artificial fixation of cliffs provides the natural sand dynamic and can improve sediment budget and beach-dune interaction (Martinez and Psuty 2004).

In former times, rocky offshore riffs stabilized sandy beaches by breaking the arriving waves in greater vicinity to the shore and reducing wave energy. These riffs were removed in the 19th and 20th century in context of the stone fishery, which used stones as construction material (Karez and Schories 2005). Some objectives in Schleswig-Holstein propose the reestablishment of artificial rocky offshore riffs as a measure of reducing wave energy at the shore, enlarging beaches, providing hard substrates for settlement of algae and stabilizing sediment load at the beach (Karez and Schories 2005; Ahrendt 2012). These riffs could also be used as diving areas, improving diving tourism at the Baltic Sea. Nevertheless, success of this measure has not yet been proven; there is much need for further research and observation.

d) Abolishment of beach cleaning measures

In the main tourist areas, beach visitors expect beaches with no natural or anthropogenic debris (Dolch 2002; Kessler 2008; Mossbauer et al. 2012). Therefore, most coastal municipalities all over the world take actions to clean beaches (Brown and McLachlan 2002; Davenport and Davenport 2006; Mossbauer et al. 2012). This procedure is costly and labour intensive and the collected material must be handled as special refuse as declared by law (BUNR 1998; MLUV 2007). This process of removing drift line material results in a decrease in beach biodiversity (Llewellyn and Shackley 1996). Furthermore, drift line material provides for less xeric abiotic conditions than sand and provides food and hiding areas for several terrestrial and marine beach fauna (Barnes and Barnes 1954; Llewellyn and Shackley 1996, Weslawski 2000; Jędrzejczak 2005). Drift line material provides nutrients and seeds, which is a prerequisite for the development of plants at the drift line zone (Cakiletea maritimae; Krisch 1990; Garcia-Mora et al. 1999). Additionally, plants are meant to be able to compensate for biomass loss (e.g. caused by trampling) as long as a sufficient nutrient source (e.g. drift line material) is provided (Gilbert et al. 2008; Seer et al. accepted 2015). The removal of drift line material not only hinders the energy and nutrient flow from sea to land, but also breaks the connectivity between different beach sites. Drift line material is of significance for beach development because it contributes to modifying the morphological structure and changes the sedimentary budget of beaches (De Falco et al. 2008; Fenu et al. 2012). The abolishment of beach cleaning measures at beaches is necessary to preserve their basic ecological functions (McLachlan et al. 2013).

In this context, some further and more integrative aspects regarding tourism, stakeholder involvement and spatial planning need to be addressed:

e) Education and participation

During a workshop that was organized within the project, the education of beach visitors, local stakeholders and especially children was considered necessary (Seer et al. 2015a). Education can help people understand the issue of nature conservation at beaches. A personal attachment of visitors to likeable organisms, e.g. birds, can help them understand the necessity of restricted

access to sensitive areas. Nature information centres, nature guiding tours, short information leaflets, newspaper articles, beach exploration and participation in research (Kessler 2008; Haller et al. 2011) might help beach visitors to reach higher education levels and increase personal interests. Reminders on the already achieved knowledge are as necessary as education. For example, signs at the beach, on parking tickets or in shops could remind visitors to respect the habitats of birds, the upper beach area or sensitive plants when entering the coast.

During interviews, local stakeholders showed a strong personal attachment to the beach (Seer et al. 2015). This underlines the necessity that measurements should be developed with a high participation of stakeholders in order to minimise their distrust, support their acceptance and includes their demands (Defeo et al. 2009; Haller et al. 2011). It has to be kept in mind that true participation also means to retreat from fixed perceptions of personal ideas and interests and, instead, work together to find an achievable solution.

f) Visitor guidance management

Visitor guidance management should aim to concentrate beach access to distinct areas (Brown and McLachlan 2002); for example, by concentrating facilities for beach visitors and transport infrastructure on some suitable beach areas for tourism (McLachlan et al. 2013). Public maps of trails and sufficient information may help visitors plan their vacation outside of closed nature conservation areas or beach sites of high nature conservation value. In addition, beach visitors should be guided by walkways over dunes or even boardwalks at the shore to concentrate pressure on distinct areas (Ciccarelli 2014). The implementation of boardwalks and walkways are also a way of helping people with disabilities enjoy the beach.

g) Marketing

Tourist marketing predetermines expectations of tourists and addresses target groups selectively. To prevent disappointment and to support the value of conservation measures, a thorough and focused tourist marketing strategy is necessary. In Schleswig-Holstein, the new tourist strategy plan even addresses ecological tourism as one of five future aims (MWAVT 2014). The focus on eco-tourists and resource-conserving recreation is one of the major tasks of the tourism agency in Schleswig-Holstein. An appropriate marketing strategy that underlines synergies of near-natural beach use might assist in connecting leisure and recreational tourism to eco-tourism.

Sustainable approaches aim on integrating social, economic and ecologic demands. The implementation of the addressed aspects in a beach management contributes to the application of sustainable management approaches and implements the maintenance of the main beach functions. To solve the remaining spatial conflict of the demanded beach uses a superregional integrated spatial planning is necessary. This identifies the most sensitive areas for tourism or nature conservation and develops appropriate measures for the specific beaches. The need for an integrated superregional spatial planning of the coast that also addresses further coastal issues and interests was already announced in several integrated coastal zone management initiatives (ICZM; Sterr 1998; Schernewski 2003). Still, ICZM is lacking governmental approval and often just

combines high economic interests where biotic aspects are easily neglected. Including ecological needs of sensitive coastal habitats such as beaches can help when considering future changes, for example, with respect to climate change issues and sea level rise.

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Picture I: **Beach visitors are advised to respect the closed off areas in the conservation area Strandseenlandschaft Schmoel near Stakendorf.**

Picture J: **Beach visitors attend a guided tour and explore beach and sea organisms near the closed off conservation area Schleimuende.**

Chapter 6

Conclusion and outlook

It can be concluded that the reduction of direct pressure of tourism by trampling on beaches is the main prerequisite for a sustainable management of beaches. The implementation of this objective in accordance with the interests of stakeholders requires a spatial regional planning that takes both environmental and economic concerns into account. This process aims at the development of adapted utilization concepts to locate and identify protection sites and implement individually customized solutions for local requirements.

Not every beach can be closed off. Therefore, it is of significant interest to identify areas where beach conservation measures can be implemented or should be implemented because of the high nature and amenity value of the site. A spatial analysis based on habitat requirements of target species is a helpful tool to identify the appropriate areas for nature conservation. They should not only comprise a suitable beach area, but also a suitable hinterland. Beach areas with a widely developed dune area in the hinterland in particular are of significant interest because they offer a complex habitat for species. They provide a well-distinguished dune chronosequence with corresponding flora and fauna and a flow of material and energy from sea to land. During flooding events, terrestrial beach fauna is able to retreat into the dune zone, while dune fauna may enter the beach to search for food. Additionally, dune species profit from drift line material that is transported into the dune area by wind and waves.

Beaches are linear habitats, which allow species to travel along the shore in two directions only. Barriers such as intensively used tourist beaches, harbours or constructions for coastal defence may easily isolate populations at the beach. Loss of connectivity between biotopes would increase the effects of disturbance and disrupt re-population of abandoned sites as well as the flow between sub-populations (Gilpin 1987; Bonte and Maes 2008; Lambeets et al. 2010). Furthermore, the size of sub-populations should at least match the minimum viable population size. Therefore, areas chosen for nature conservation need to be connected or in close proximity to allow gene flow between sub-populations of species or provide stepping-stones between populations. An integration of these tasks (enhanced biotope connectivity) to the coastline and the maintenance of basic ecological functioning of beaches can better be reached by conservation efforts focusing on the landscape level than on small scale planning (Faith and Walker 1996; Wessels et al. 1999; Carboni et al. 2009).

An integrated management plan includes the desires of stakeholders and identifies beaches of tourism priority. This gives tourist marketing and local stakeholders planning security. A focus of tourism facilities to distinct areas provides a concentration of tourism as well as cash resources for the municipalities. At the Baltic Sea coast of Schleswig-Holstein, it is highly unlikely and not an objective to implement conservation measures at tourism hot spots. However, especially in these areas, improved tourism guidance with clearly defined paths from the dike through the beach ridge to the beach would help to provide “stepping-stones” for flora and fauna along the shore. A process-orientated participation of stakeholders is essential for the development of new nature conservation areas and for the development of beach management solutions to identify subjects of conflicts early and gain the trust of planning partners.

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Picture K: **Visitor management by fixed routing through the dune and foredune area of the conservation area Kleiner Binnensee bei Behrensdorf.**

Picture L: **Partly closed beach with closed upper shore and accessible lower shore and water side at the beach close to the conservation area Wasservogelreservat Wallnau at the island Fehmarn.**

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Erklärung

Hiermit erkläre ich, dass ich die vorliegende Dissertation eigenständig und ohne fremde Hilfe angefertigt habe. Arbeiten Dritter wurden entsprechend zitiert. Die Arbeit ist unter Einhaltung der Regeln der guten wissenschaftlichen Praxis der Deutschen Forschungsgemeinschaft entstanden.

Diese Dissertation wurde bisher in dieser oder ähnlicher Form noch bei keiner anderen Institution eingereicht. Ich habe bisher keine erfolglosen Promotionsversuche unternommen.

Da es sich bei der vorliegenden Arbeit um eine kumulative Dissertation handelt sind einzelne Kapitel in namhaften wissenschaftlichen Journals veröffentlicht oder zur Veröffentlichung vorgesehen. Dies ist entsprechend gekennzeichnet.

Kiel, den

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(Franziska K. Seer)